Reptile dispersal and demography after fire: process-based knowledge to assist fire management for biodiversity

Annabel L. Smith

A thesis submitted for the
degree of Doctor of Philosophy of
The Australian National University

Australian
National
University

March 2012

Cover images: striped skink (*Ctenotus atlas*), the starred knob-tailed gecko (*Nephrurus stellatus*), the mallee tree dragon (*Amphibolurus norrisi*), and a mallee woodland in southern Australia (photos A.L. Smith).

Declaration

This thesis is my own work, except where otherwise acknowledged (see Preface and Acknowledgements).

Annabel Smith
March 2012

Table of Contents

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 7

Chapter 8

Appendix A

Preface

This thesis consists of six papers that communicate the research I undertook for my doctoral program (Chapters 2-7). These papers are framed by a brief introduction (Chapter 1) and conclusion (Chapter 8) which explain the relationships between the papers, and place the thesis in a broad ecological context. Two papers have been published (Chapters 4 and 5) and the remaining papers have been prepared for publication, but not yet submitted to journals. The papers were written to stand alone, so references have been provided at the end of each chapter. I have also provided a comprehensive reference list in Appendix A.

My project was part of a broader study on the fire ecology of plants, birds and reptiles, funded predominantly by an Australian Research Council grant to Don Driscoll and a group of co-investigators. Other funding partners are acknowledged at the end of each chapter. This project followed on from a previous study conducted by Don Driscoll with which I was also involved (see Driscoll et al. 2012, *Biodivers. Conserv.*). Chapters 2 and 3 include some data collected during the previous study, but I collected the majority of the data presented in the thesis during my PhD program. I designed my research agenda within the framework for the broader fire ecology project in consultation with my supervisors Don Driscoll, Michael Bull and Michael Gardner. I conducted all of the field work for my project and coordinated teams of volunteers to assist me.

Of the DNA samples used for this thesis, I collected 79 % in the field and 21 % from tissue stored at the South Australian Museum (SAM) that were collected during the previous study. I conducted the molecular marker development, DNA extractions, and PCR amplifications with technical advice from Michael Gardner and staff at the SAM, and I outsourced capillary electrophoresis to the Australian Genome Research Facility. I planned and conducted all statistical analyses in consultation with my supervisors and I wrote the R scripts to analyse the data and create the figures. The chapters within this thesis were conceived and written by me with scientific and editorial input from my supervisors. All co-authors are listed at the beginning of each chapter, and all due acknowledgements are given at the end of each chapter.

Acknowledgements

My biggest thanks go to my primary supervisor Don Driscoll for supporting, challenging, and inspiring me throughout my doctoral program. My co-supervisors Michael Bull and Michael Gardner have also given me constant support and encouragement. I continually appreciated the prompt, thorough, and insightful feedback from all three of my supervisors. It has been a privilege to work as part of this team.

The people at the South Australian Museum helped me solve countless molecular and taxonomic problems, particularly Mark Hutchinson, Kathy Saint, Terry Bertozzi, and Steve Donnellan. I was lucky to be involved in a research group including Ross Bradstock, David Keith, Sonia Kleindorfer and Andrew Lowe who all gave me wise advice during my program. My fire-ecology peers Simone Dalgairns, Bianca Dunker, Rebecca Gibson, Juliana Lazzari, and Brendon Meulders gave me valuable insights into the broader context of our research. Sally South, Greg Johnston, Luisa Teasdale, and Handoko Wahjudi worked on field projects related to mine that deepened our understanding of the ecosystem.

Thanks to all of my colleagues in the Conservation and Landscape Ecology group at ANU and in the Bull Lab at Flinders University. Dale Burzacott, Dick Edyvean and Bob Knibbs provided logistical support at the outset of my project. Later, Martin Westgate was my R code mentor, John Stein was my GIS guru, and AJ Carter, Pia Lentini, Karen Stagoll, and Ingrid Stirnemann all provided useful advice on overcoming a mixed-bag of thesis-related obstacles. Sam Banks, Wade Blanchard, Rachael Dudaniec, and Hwan-Jin Yoon gave me analytical and statistical advice. The South Australian Department of Environment and Natural Resources helped me with access to field sites, spatial data, and research permits. Special thanks go to Joe Tilley from the Pt. Lincoln branch for reliable support in the field and for sharing his expert fire knowledge.

I am immensely grateful to over 40 people who volunteered to help me collect data in very challenging field conditions. They are acknowledged individually at the end of Chapter 4. Some people gave me sustained support and friendship in the field that I could not have done without: Samantha Blight, Simone Dalgairns, Juliana Lazzari, Kevin Mayes, Andrew Murphy, and Catherine Whitehead. The Eyre Peninsula community made me feel at home in the field, particularly Brian Peters, Karen Peters, Malcolm Peters, Frank Schaefer, Jo Schaefer, John Schaefer, Judy Schaefer, Craig Wheare, and Georgie Wheare.

Thanks to my family, friends, and family-like friends. These people are my fat, giggling fairy: Kym Abrams, Tessa Bradford, Sophie Clement, Simone Dalgairns, Andrew Dobson, Liz Dobson, Toby Dobson, Rachael Dudaniec, Rebecca Gibson, Ingerid Julie Hagen, Sergio Juárez, Juliana Lazzari, Rosy Lazzari, Thea Lazzari, David Leigh, Nicole Maron, Kevin Mayes, Alex Smith, Beth Smith, Joey Smith, Quentin Smith, John Stein, Ingrid Stirnemann, Kathy Suen, Rachel Walpole, Martin Westgate, David Wong, and Edwin Wong.

Abstract

The disruption of natural fire regimes has threatened animal species in many ecosystems around the world. A combination of prescribed burning and fire suppression is often used to promote successional variation in vegetation (i.e. fire mosaics), with little knowledge of how this will affect animal persistence. Understanding the processes that govern species responses to fire regimes is essential to build a predictive capacity for ecological fire management. I examined life-history, demographic (survival, reproduction and mortality) and dispersal attributes of reptiles to investigate mechanisms of fire responses in reptiles. I studied reptiles in conservation reserves of semi-arid southern Australia dominated by mallee vegetation (multi-stemmed *Eucalyptus spp*. with a shrubby understory). An introduction describes the ecological and management context of my research (Chapter 1). A community-level framework was used to determine if a generalised model of fire responses could be developed based on traits shared by groups of species (Chapters 2-3). I found a number of fire responses in reptiles that were previously undetected in analyses of smaller, but substantial subsets of the same data (Chapter 2). Nocturnal burrowers tended to be early-successional, while diurnal leaf-litter dwellers tended to be late successional, but a trait-based model of succession had limited power to describe responses among the community. I also documented some observations that suggested non-burrowing reptiles were more vulnerable to mortality during wildfire than burrowers (Chapter 3). A species-level framework was then used to examine variation in demographic and dispersal attributes within species among different post-fire successional stages (Chapters 4-7). These studies focussed on three species with significant and contrasting responses to fire: *Amphibolurus norrisi* (Agamidae; mid/late successional species), *Ctenotus atlas* (Scincidae; late successional) and *Nephrurus stellatus* (Gekkonidae; early/mid successional). Using mark-recapture modelling (Chapter 4), I described changes in abundance of *N. stellatus* that incorporated detectability, and showed that variation in survival and fecundity are possible drivers of this species strong population response to fire. Microsatellite DNA data were then used to examine gene flow in the three target species and gain insights into the effects of fire on dispersal. Chapter 5 begins this section with a description of the markers I used to generate the genetic data. I then used spatial models of landscape resistance to assess the importance of post-fire succession and other landscape features (e.g. topography) on gene flow in the three species (Chapters 6 and 7). For *N. stellatus* these analyses were combined with direct observations of movement (Chapter 6). Results showed that long-unburnt vegetation restricts dispersal in *N. stellatus*, which may result from, or contribute to its decline in population density with increasing time since fire. In Chapter 7 I found that fire affected gene flow in *A. norrisi*, but not in *C. atlas*, while genetic diversity in both species was affected by post-fire succession. My thesis demonstrated how examining demographic and dispersal attributes of reptiles can give insights into the mechanisms underlying species responses to fire. I concluded by providing management recommendations and highlighting key points for future research on fire ecology (Chapter 8).

Chapter 1

The need for a process-based understanding of fire ecology in reptiles

Introduction

Fire is a common agent of disturbance in ecosystems around the world, including the mallee woodlands of semi-arid southern Australia (Photo A. Castañeda, taken in March 2008 at Hambidge Wilderness Area on the Eyre Peninsula).

1.1 Fire management and biodiversity conservation

Ecological communities in many regions of the world experience successional changes in species composition and habitat structure driven by natural fire regimes (Gill 1975; Bowman et al. 2009). However, widespread changes in land use and fire management practices, particularly in the past century, have altered the way that fire affects biodiversity. In some regions, active fire suppression has led to declines of species that rely on open habitats created by recurrent fire (Templeton et al. 2001; Betts et al. 2010; Gregory et al. 2010). In other regions, frequent burning has caused declines in species that need unburnt vegetation to persist (Lyet et al. 2009; Sanz-Aguilar et al. 2011; Woinarski et al. 2011). In addition to these temporal changes in fire regimes, the modification of spatial landscape configuration from habitat loss and fragmentation has changed how fire affects the biota (Cochrane 2001; Lawson et al. 2010; Wang & Cumming 2010; Parsons & Gosper 2011). To effectively conserve biodiversity, new, evidence-based approaches to managing fire in contemporary landscapes are needed (Keith et al. 2002; Tabarelli & Gascon 2005).

Conceptual and simulation models can be used to synthesise information about ecological fire responses so that management agencies can predict biodiversity outcomes of under different circumstances (e.g. Moreira et al. 2009). The framework for applying fire response models has been well developed for plants at both the species (e.g. Bradstock et al. 2006) and the community level (e.g. Keith et al. 2007). In comparison, the development of models to predict animal responses to fire has been much slower. One reason for this is that the recovery of animal species after fire is often assumed to follow the regeneration of suitable habitat (Parr & Andersen 2006; Clarke 2008). For example, Fox (1982) described a conceptual model for small mammals based on observations that the recovery of species corresponded to successional changes in their habitat after fire. However, recent studies on other mammals and reptiles, have failed to show fire response patterns that would be predicted by Fox's (1982) habitat accommodation model (Driscoll & Henderson 2008; Lindenmayer et al. 2008; Di Stefano et al. 2011; Kelly et al. 2011). Understanding attributes inherent to animals that influence their fire responses is necessary to move beyond models based solely on habitat suitability (Clarke 2008).

Models of plant regeneration after fire are based on a solid understanding of variation in survival, reproduction and regeneration among different species (e.g. seeders vs. resprouters, Pausas et al. 2004). In contrast, we have very little understanding of the life history and demographic attributes of animals that underlie their responses to fire (Whelan et al. 2002; Clarke 2008). Regularly burnt habitats are spatially heterogeneous in their nature, and dispersal is essential for animal species to maintain connectivity in patchy habitats (Thomas 2000; Schooley & Wiens 2004). Understanding dispersal across fire mosaics (i.e. habitats at different stages of successional development) is thus particularly important for guiding fire management. Other attributes that are likely to be important for animals include mortality during fire, survival in the post-fire environment, and rates of population growth and reproduction (Whelan et al. 2002; Clarke 2008; Driscoll et al. 2010). Developing knowledge of the processes governing animal responses to fire is critical for incorporating the needs of animals into fire management plans (Friend 1993; Whelan et al. 2002; Clarke 2008; Driscoll et al. 2010).

The species most likely to decline under inappropriate fire regimes are "fire specialists", that is, those species that specialise on vegetation that develops at a particular successional stage (Driscoll & Henderson 2008). Reptiles are often reported to be fire specialists (Mushinsky 1985; Greenberg et al. 1994; Letnic et al. 2004; Lindenmayer et al. 2008), but few studies have investigated the attributes of reptiles that underlie their relationships to post-fire succession. Reptiles comprise a substantial component of the biodiversity in many fire prone ecosystems, and have an important functional role in food webs and soil disturbance (Abensperg-Traun & Steven 1997; Eldridge & James 2009). A detailed investigation of demography and dispersal in reptiles is needed to ensure that fire management is conducted at scales that will ensure their persistence in fire prone landscapes.

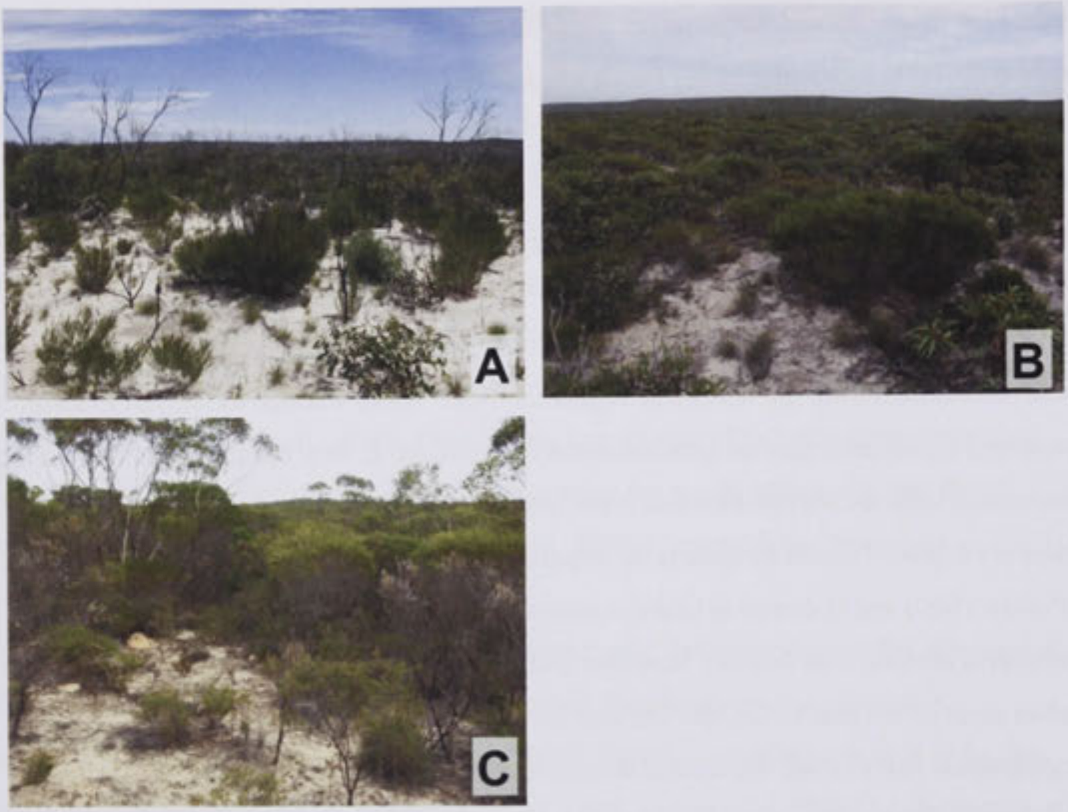
The aim of my thesis was to investigate relationships between fire regimes and the dispersal, demographic, and life history attributes of reptiles in order to advance our understanding of the processes behind animal responses to fire. I addressed issues of habitat use, mortality during fire, post-fire survival, reproduction, and population density of reptiles, but there was a strong focus in my thesis on the effects of fire on dispersal. Almost nothing is known about how fire effects dispersal in reptiles (but see Schrey et al. 2011; Templeton et al. 2011) so a detailed investigation into this important life history attribute was essential. I took a multi-disciplinary approach to addressing these varied and complex problems, including community level trait-based analyses, species specific mark-recapture analysis of abundance, survival and movement, an observational survey of post-fire mortality, and molecular analyses of landscape-scale gene flow to understand dispersal. In the following section I will explain my research approach and the structure of my thesis in more detail.

1.2 Addressing issues in reptile fire ecology

I studied reptiles in conservation reserves on the Eyre Peninsula, South Australia, where mallee woodlands are the dominant vegetation type. These woodlands consist of multi-stemmed *Eucalyptus* species (predominantly *E. costata*, *E. brachycalyx* and *E. socialis*), associated with the shrubs *Melaleuca uncinata*, and *Callitris verrucosa*. The spiky hummock grass *Triodia irritans* is an important habitat plant for many reptile species (Pianka 1969) and is common in the reserves on the Eyre Peninsula. The region has a semi-arid climate with hot, dry summers and cool, relatively wet winters (June-August) when most of the rain falls (300-400 mm on average) (Schwerdtfeger 1985). The main topographic features are white sand dunes, occurring in either large, parabolic fields or longitudinal ridges interspersed by hard, reddish-brown swales. Over 60 % of the native vegetation on the Eyre Peninsula has been cleared for agriculture, with the remaining vegetation restricted to a few large reserves (> 30,000 ha) and several small remnants (< 1,000 ha) (ANVA 2001).

Summer lightning is the most common ignition source of mallee and typically results in large, severe wildfires on a decadal time scale (Bradstock et al. 2005). As a consequence, the mallee reserves of the Eyre Peninsula have complex fire mosaics, spanning a range of times since fire and fire frequencies. Ongoing records of fires are kept by the South Australian Department of Environment and Natural Resources (DENR 2011) and fire histories of the reserves have been mapped using Landsat images and air photos dating back to the 1970s and 1950s, respectively. Fire drives marked changes in vegetation structure of mallee (Fig. 1.1), promoting spatial heterogeneity at a landscape scale. The complex fire history, combined with a diverse reptile fauna (Driscoll & Henderson 2008), and the ability to replicate studies in multiple reserves at a regional level, makes the Eyre Peninsula an ideal location for studying fire ecology in reptiles.

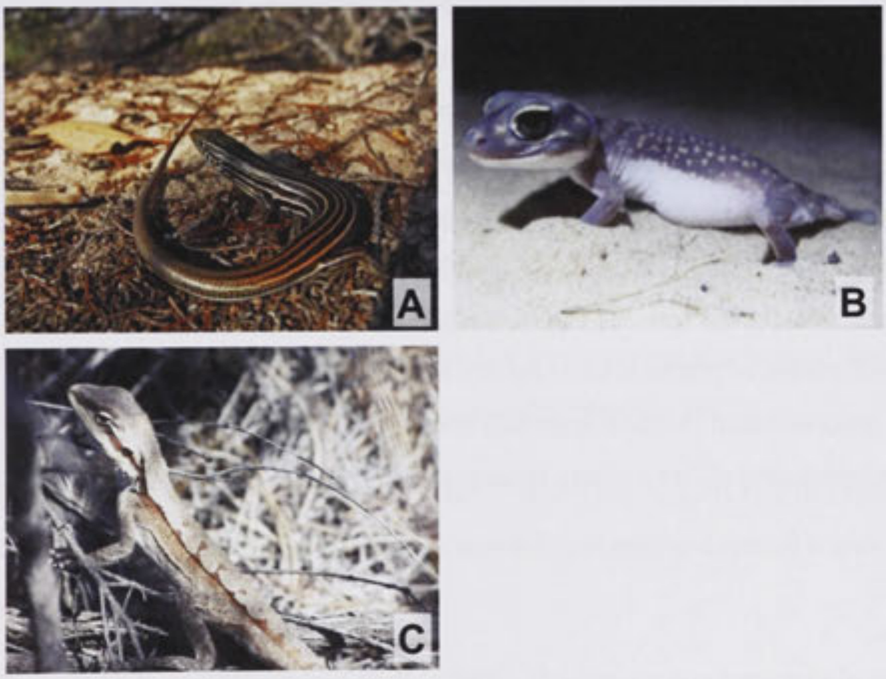
Fig. 1.1 Mallee vegetation (A) three, (B) ten, and (C) 43 years after fire (Photos: A.L. Smith taken in Nov 2009 at Hincks Wilderness Area on the Eyre Peninsula).



I used two general frameworks to study the processes behind reptile fire responses. The first was a community-level framework which I used in Chapters 2 and 3 to examine if a generalised model of fire responses could be developed based on traits shared by groups of species. In Chapter 2 this framework was applied to a large data set (4796 individuals recorded over six years) from the mallee reptile community to determine if habitat use and life history traits related to variation in abundance with time since fire. In Chapter 3 I examined if there were any shared traits among reptile species that experienced mortality during a severe summer wildfire. In the following chapters of my thesis I used a species-level framework in order to examine variation in life history and dispersal attributes within species among different successional stages.

I conducted the species-level studies on three mallee lizard species (Fig. 1.2): (A) *Ctenotus atlas* (Scincidae), (B) the starred knob-tailed gecko, *Nephrurus stellatus* (Gekkonidae), and (C) the mallee tree-dragon, *Amphibolurus norrisi* (Agamidae). These species were targeted because they had previously shown significant responses to time since fire that differed among the three species (Driscoll & Henderson 2008). *Ctenotus atlas* was uncommon in the first three years after fire, and increased to a peak in abundance at 5-7 years after fire (Driscoll & Henderson 2008). *Nephrurus stellatus* was reported to be more common in recently burnt (≤ 7 years since fire) than long unburnt (≥ 18 years) mallee consistently in four reserves on the Eyre Peninsula (Driscoll & Henderson 2008). The response of *Amphibolurus norrisi* varied across the Eyre Peninsula, being more abundant in 30 year old mallee at one location and in 5 year old mallee at another location. This range of responses to fire allowed me to examine successional variation in life history and dispersal attributes of the three species, and potentially uncover some of the processes behind their population response to fire regimes.

Fig. 1.2 Three reptile species were targeted for detailed studies: (A) *Ctenotus atlas*, (B) *Nephrurus stellatus*, and (C) *Amphibolurus norrisi* (Photos: A.L. Smith).



The first of the species-level studies (Chapter 4) used data from mark-recapture surveys to examine successional variation in survival, population density and reproductive capacity of *N. stellatus* (Smith et al. 2012). Microsatellite DNA data were then used to examine successional changes in gene flow and gain insights into the effects of fire on dispersal in all three target species. Chapter 5 begins this section with a description of the markers I used to generate the genetic data (Smith et al. 2011). In Chapters 6 and 7 I used spatial models of landscape resistance to directly assess the importance of post-fire succession and other landscape features (e.g. topography) on gene flow in the three target species. For *N. stellatus*, I combined results from analysis of landscape genetic structure and with direct observations of movement to examine dispersal across fire mosaics (Chapter 6). Chapter 7 follows with a comparison of landscape genetic structure in *C. atlas* and *A. norrisi*. The final chapter of my thesis (Chapter 8) summarises the main results from my research, presents recommendations for management, and highlights important directions for future research.

1.3 Benefits to fire management

Models to predict the effects of fire on biodiversity rely on understanding the processes that drive species responses to post-fire succession (Whelan et al. 2002; Clarke 2008; Driscoll et al. 2010). My thesis will contribute important knowledge about how demographic and dispersal attributes vary among and within reptile species in fire prone ecosystems. This is a critical step towards developing a conceptual framework to guide fire management for animal conservation. For example, knowledge of dispersal variation across patchy fire mosaics will help to predict if prescribed fires will create barriers to dispersal in reptiles. In addition, simulation models that are used to quantify the effects of prescribed burning regimes (e.g. Bradstock et al. 2005) need accurate species-level data to be parameterised. The results presented in my thesis will therefore assist in the development of practical tools for fire management. In addition, my thesis demonstrates a process-based research approach that can be used in future studies to improve our understanding of fire ecology in animals.

1.4 References

Abensperg-Traun M. and Steven D. (1997). Ant- and termite-eating in Australian mammals and lizards: a comparison. *Australian Journal of Ecology* 22: 9-17.

ANVA (2001). *Australian Native Vegetation Assessment.* National Land and Water Resources Audit and Commonwealth of Australia, Canberra, ACT.

Betts M.G., Hagar J.C., Rivers J.W., Alexander J.D., McGarigal K. and McComb B.C. (2010). Thresholds in forest bird occurrence as a function of the amount of early-seral broadleaf forest at landscape scales. *Ecological Applications* 20: 2116-2130.

Bowman D.M.J.S., Balch J.K., Artaxo P., Bond W.J., Carlson J.M., Cochrane M.A., D'Antonio C.M., DeFries R.S., Doyle J.C., Harrison S.P., Johnston F.H., Keeley J.E., Krawchuk M.A., Kull C.A., Marston J.B., Moritz M.A., Prentice I.C., Roos C.I., Scott A.C., Swetnam T.W., van der Werf G.R. and Pyne S.J. (2009). Fire in the Earth system. *Science* 324: 481-484.

Bradstock R.A., Bedward M. and Cohn J.S. (2006). The modelled effects of differing fire management strategies on the conifer *Callitris verrucosa* within semi-arid mallee vegetation in Australia. *Journal of Applied Ecology* 43: 281-292.

Bradstock R.A., Bedward M., Gill A.M. and Cohn J.S. (2005). Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. *Wildlife Research* 32: 409-423.

Clarke M.F. (2008). Catering for the needs of fauna in fire management: science or just wishful thinking? *Wildlife Research* 35: 385-394.

Cochrane M.A. (2001). Synergistic interactions between habitat fragmentation and fire in evergreen tropical forests. *Conservation Biology* 15: 1515-1521.

DENR (2011). *NatureMaps* Department of Environment and Natural Resources. http://www.naturemaps.sa.gov.au/ (accessed September 2011).

Di Stefano J., Owen L., Morris R., Duff T. and York A. (2011). Fire, landscape change and models of small mammal habitat suitability at multiple spatial scales. *Austral Ecology* 36: 638-649.

Driscoll D.A. and Henderson M.K. (2008). How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model. *Biological Conservation* 141: 460-471.

Driscoll D.A., Lindenmayer D.B., Bennett A.F., Bode M., Bradstock R.A., Cary G.J., Clarke M.F., Dexter N., Fensham R., Friend G., Gill A.M., James S., Kay G., Keith D.A., MacGregor C., Russell-Smith J., Salt D., Watson J.E.M., Williams R.J. and York

A. (2010). Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation* 143: 1928-1939.

Eldridge D.J. and James A.I. (2009). Soil-disturbance by native animals plays a critical role in maintaining healthy Australian landscapes. *Ecological Management and Restoration* 10: S27-S34.

Fox B.J. (1982). Fire and mammalian secondary succession in an Australian coastal heath. *Ecology* 63: 1332-1341.

Friend G.R. (1993). Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: a review. *Biological Conservation* 65: 99-114.

Gill A.M. (1975). Fire and the Australian flora: a review. *Australian Forestry* 38: 4-25.

Greenberg C.H., Neary D.G. and Harris L.D. (1994). Effect of high-intensity wildfire and silvicultural treatments on reptile communities in sand-pine scrub. *Conservation Biology* 8: 1047-1057.

Gregory N.C., Sensenig R.L. and Wilcove D.S. (2010). Effects of controlled fire and livestock grazing on bird communities in east African savannas. *Conservation Biology* 24: 1606-1616.

Keith D.A., Holman L., Rodoreda S., Lemmon J. and Bedward M. (2007). Plant functional types can predict decade-scale changes in fire-prone vegetation. *Journal of Ecology* 95: 1324-1337.

Keith D.A., Williams J.E. and Woinarski J.C.Z. (2002). Fire management and biodiversity conservation: key approaches and principles. In: *Flammable Australia: the fire regimes and biodiversity of a continent.* (eds. Bradstock RA, Williams JE, Gill AM). Cambridge University Press, Cambridge.

Kelly L.T., Nimmo D.G., Spence-Bailey L.M., Haslem A., Watson S.J., Clarke M.F. and Bennett A.F. (2011). Influence of fire history on small mammal distributions: insights from a 100-year post-fire chronosequence. *Diversity and Distributions* 17: 462-473.

Lawson D.M., Regan H.M., Zedler P.H. and Franklin J. (2010). Cumulative effects of land use, altered fire regime and climate change on persistence of *Ceanothus verrucosus*, a rare, fire-dependent plant species. *Global Change Biology* 16: 2518-2529.

Letnic M., Dickman C.R., Tischler M.K., Tamayo B. and Beh C.-L. (2004). The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *Journal of Arid Environments* 59: 85-114.

Lindenmayer D.B., Wood J.T., MacGregor C., Michael D.R., Cunningham R.B., Crane M., Montague-Drake R., Brown D., Muntz R. and Driscoll D.A. (2008). How predictable are reptile responses to wildfire? *Oikos* 117: 1086-1097.

Lyet A., Cheylan M., Prodon R. and Besnard A. (2009). Prescribed fire and conservation of a threatened mountain grassland specialist: a capture-recapture study on the Orsini's viper in the French alps. *Animal Conservation* 12: 238-248.

Moreira F., Catry F., Duarte I., Acácio V. and Silva J.S. (2009). A conceptual model of sprouting responses in relation to fire damage: an example with cork oak (*Quercus suber* L.) trees in southern Portugal. *Plant Ecology* 201: 77-85.

Mushinsky H.R. (1985). Fire and the Florida sandhill herpetofaunal community: with special attention to responses of *Cnemidophorus sexlineatus*. *Herpetologica* 41: 333-342.

Parr C.L. and Andersen A.N. (2006). Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Conservation Biology* 20: 1610-1619.

Parsons B.C. and Gosper C.R. (2011). Contemporary fire regimes in a fragmented and an unfragmented landscape: implications for vegetation structure and persistence of the fire-sensitive malleefowl. *International Journal of Wildland Fire* 20: 184-194.

Pausas J.G., Bradstock R.A., Keith D.A., Keeley J.E. and GCTE (2004). Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* 85: 1085-1100.

Pianka E.R. (1969). Habitat specificity, speciation, and species density in Australian desert lizards. *Ecology* 50: 498-502.

Sanz-Aguilar A., Anadón J.D., Giménez A., Ballestar R., Graciá E. and Oro D. (2011). Coexisting with fire: the case of the terrestrial tortoise *Testudo graeca* in mediterranean shrublands. *Biological Conservation* 144: 1040-1049.

Schooley R. and Wiens J.A. (2004). Movements of cactus bugs: patch transfers, matrix resistance, and edge permeability. *Landscape Ecology* 19: 801-810.

Schrey A.W., Fox A.M., Mushinsky H.R. and McCoy E.D. (2011). Fire increases variance in genetic characteristics of Florida Sand Skink (*Plestiodon reynoldsi*) local populations. *Molecular Ecology* 20: 56-66.

Schwerdtfeger P. (1985). Climate. In: *Natural history of Eyre Peninsula.* (eds. Twidale CR, Tyler MJ, Davies M), pp. 89-104. Royal Society of South Australia, Adelaide, SA.

Smith A.L., Bull C.M. and Driscoll D.A. (2012). Post-fire succession affects abundance and survival but not detectability in a knob-tailed gecko. *Biological Conservation* 145: 139-147.

Smith A.L., Gardner M.G., Bull C.M. and Driscoll D.A. (2011). Primers for novel microsatellite markers in "fire-specialist" lizards (*Amphibolurus norrisi, Ctenotus atlas* and *Nephrurus stellatus*) and their performance across multiple populations. *Conservation Genetics Resources* 3: 345-350.

Tabarelli M. and Gascon C. (2005). Lessons from fragmentation research: improving management and policy guidelines for biodiversity conservation. *Conservation Biology* 19: 734-739.

Templeton A.R., Brazeal H. and Neuwald J.L. (2011). The transition from isolated patches to a metapopulation in the eastern collared lizard in response to prescribed fires. *Ecology* 92: 1736-1747.

Templeton A.R., Robertson R.J., Brisson J. and Strasburg J. (2001). Disrupting evolutionary processes: the effect of habitat fragmentation on collared lizards in the Missouri Ozarks. *Proceedings of the National Academy of Science, USA.* 98: 5426-5432.

Thomas C.D. (2000). Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 267: 139-145.

Wang X. and Cumming S.G. (2010). Configuration dynamics of boreal forest landscapes under recent fire and harvesting regimes in western Canada. *Landscape Ecology* 25: 1419-1432.

Whelan R.J., Rodgerson L., Dickman C.R. and Sutherland E.F. (2002). Critical life cycles of plants and animals: developing a process-based understanding of population changes in fire-prone landscapes. In: *Flammable Australia: the fire regimes and biodiversity of a continent.* (eds. Bradstock RA, Williams JE, Gill AM). Cambridge University Press, Cambridge.

Woinarski J.C.Z., Legge S., Fitzsimons J.A., Traill B.J., Burbidge A.A., Fisher A., Firth R.S.C., Gordon I.J., Griffiths A.D., Johnson C.N., McKenzie N.L., Palmer C., Radford I., Rankmore B., Ritchie E.G., Ward S. and Ziembicki M. (2011). The disappearing mammal fauna of northern Australia: context, cause, and response. *Conservation Letters* 4: 192-201.

Chapter 2

A six-year study reveals previously undetected responses to fire in reptiles

Research Paper

Co-authors:
C. Michael Bull
Don A. Driscoll

Habitat with over 30 years since fire may be important for mallee reptiles that inhabit leaf litter, such as Lerista distinguenda *(Photo A.L. Smith).*

2.1 Abstract

Understanding contrasting responses to fire among animal communities and the mechanisms governing these responses is essential for successful ecological fire management. We used data from an Australian mallee woodland reptile community (4796 records collected over six years) to: (i) determine if previous studies using smaller subsets of the same data correctly identified the number of species with significant abundance responses to time since fire (TSF); and (ii) investigate whether habitat use and life history traits could reliably predict reptile responses to fire. We modelled the abundance of 16 reptile species as a function of TSF using generalised linear mixed models and tested for relationships between fire responses and ecological traits. Our analysis revealed two important results. First, while the responses of five species to TSF were consistent with previous studies, we found an additional eight species with significant responses to TSF that were not found using smaller data sets. The majority of species analysed (13/16) had a significant response to TSF, with peak abundances ranging from one year to 50 years after fire. Second, ecological traits of individual lizard species had little statistical power to explain fire responses, but we observed a general trend for nocturnal burrowers to be early successional and for diurnal leaf-litter dwellers to be late successional. Immense survey effort is required to detect fire responses in reptiles, highlighting the need for management decisions to be based on large data sets. Most common mallee reptile species may be at risk of decline under inappropriate fire regimes. For future research, inclusion of more detailed species traits and habitat measurements will probably improve our ability to predict biodiversity outcomes under different fire regimes.

2.2 Introduction

Animal species in many ecosystems are threatened by altered fire regimes (Brisson et al. 2003; Pons & Clavero 2010; Woinarski et al. 2011), and inappropriate management is often responsible. Frequent prescribed burning has probably led to declines in alpine reptiles of Europe (Lyet et al. 2009) and mammals of northern Australia (Woinarski et al. 2004b). Conversely, long-term active fire suppression has probably caused declines in bird communities of North America (Betts et al. 2010) and Africa (Gregory et al. 2010). Prescriptions to increase or suppress burning of natural vegetation are often politically motivated and given without a scientific basis (e.g. VBRC 2010). Implementing management without understanding its ecological consequence or effectiveness could alter ecological communities, reduce biodiversity or, at the very least, could waste resources (Parr & Andersen 2006; Driscoll et al. 2010a; Andersen et al. 2012).

With sufficient knowledge, prescribed burning can be used to restore natural processes. In North American glades, prescribed fire successfully promoted dispersal and restored the natural metapopulation structure of the collared lizard (Templeton et al. 2011). Such successful fire management relies on understanding both the extent to which animal species specialise on a post-fire habitat stage, and the contrasting responses to fire among species in the ecological community (Driscoll et al. 2010b). Currently, this information is unavailable for many animal communities in fire-prone regions (Bradstock & Cohn 2002; Clarke 2008). For successful conservation, it is critical that fire management is based on accurate, quantitative descriptions of ecological fire responses for many species within a community.

Predicting the effects of changing fire regimes on an ecosystem can be assisted by conceptual models which describe biodiversity outcomes under different circumstances (e.g. Letnic et al. 2004). The development of such models for animal communities has been impeded by the simplistic assumption that animal succession can be predicted by vegetation changes (Clarke 2008). In some studies of reptiles, recovery after fire was predictable. For example, in mallee vegetation of southern Australia, Caughley (1985) found that burrowing reptiles specialised on early successional habitats after fire, reptiles that lived in *Triodia* grasses showed mid successional responses, and leaf-litter dwellers were late successional. Letnic et al. (2004) made further developments by showing that nocturnal reptile species recolonised burned areas more quickly than diurnal species, probably because they had less need for shelter from above ground vegetation while active. However, more recent evidence suggests that reptile succession after fire in other systems, including other mallee regions, is not predictable for many species using these models (Driscoll & Henderson 2008; Lindenmayer et al. 2008). Further research is needed to resolve this conflict and advance our understanding of the mechanisms governing animal succession.

Another reason for the slow development of animal succession models, is that collecting sufficient data to make reliable inferences, particularly for vertebrates, can be laborious and difficult (Clarke 2008). Rare animals often go unstudied (Manley et al. 2004) and incorrect inferences can be drawn from sparse data (Doak et al. 2005). Using power analysis, Woinarski (2004a) demonstrated that the survey effort required to detect fire responses in reptiles is substantially greater than employed in many surveys. There is an urgent need for long-term, intensive data collection to improve our understanding of fire ecology in animal communities (Woinarski et al. 2004a).

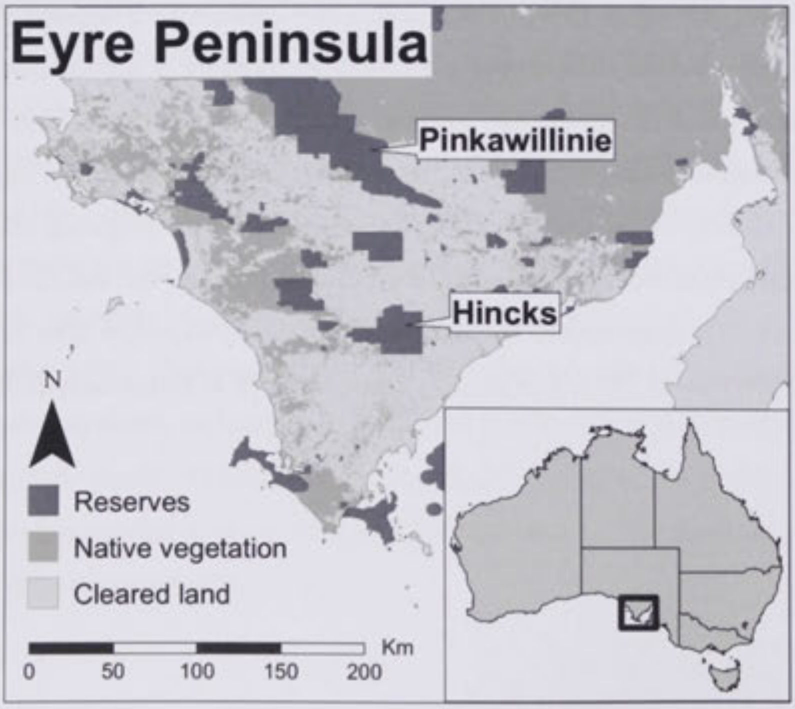
The broad objective of this study was to describe the response of an Australian reptile community to post-fire succession using a large data set collected over six years and determine if species traits could explain their responses. Our first aim was to expand our understanding of which reptile species were affected by post-fire succession, from two previous studies which used smaller subsets of the data presented in this study. Nine out of 16 (Driscoll & Henderson 2008) and 15 out of 17 species (Driscoll et al. 2012) were previously reported to show no detectable response to succession. These results suggest that most common reptile species may not be threatened by variation in fire management practices. However, both of these studies emphasised the need for larger data sets to examine reptile responses to succession with increased statistical power (Driscoll & Henderson 2008; Driscoll et al. 2012). In the current study, we combined data from two previously reported consecutive two-year studies (Driscoll and Henderson 2008, N = 1585; Driscoll et al. 2012, N = 2060) with a further two years of survey data (and a further 1151 reptile records) to increase the statistical power of the analyses, and potentially increase the number of species that we could detect as responding to habitat changes following fire. Our second aim was to investigate possible mechanisms of succession among those species by investigating relationships between species traits and fire responses. We examined habitat use and life history traits that were previously suggested to be important for reptile succession after fire (Caughley 1985; Friend 1993; Letnic et al. 2004; Driscoll & Henderson 2008).

2.3 Methods

2.3.1 Study region

We studied reptiles in two reserves on the Eyre Peninsula, South Australia (Fig. 2.1): Hincks Wilderness Area (33°45' S, 136°03' E; 66658 ha) and Pinkawillinie Conservation Park (32°54' S, 135°53' E; 130148 ha). The region is semi-arid, with an average annual rainfall of 340 mm at Hincks and 302 mm at Pinkawillinie. The main topographic features are white sand dunes, occurring in either large, parabolic fields or longitudinal ridges interspersed by hard, reddish-brown swales (Twidale & Campbell 1985). Mallee, characterised by multi-stemmed *Eucalyptus spp.*, is the dominant vegetation type in the reserves, where *E. costata* and *E. socialis* are commonly associated with the shrubs *Melaleuca uncinata* and *Callitris verrucosa* (Specht 1972; Robinson & Heard 1985). The spiky hummock grass *Triodia irritans* forms an important habitat for many reptile species, and is common in both reserves. Summer lightning is the most common ignition source of mallee which typically results in large, severe wildfires on a decadal time scale (Bradstock & Cohn 2002).

Fig. 2.1 Location of Hincks Wilderness Area and Pinkawillinie Conservation Park where reptiles were studied on the Eyre Peninsula, South Australia.



2.3.2 Data collection

We defined a field season as the spring/summer period from November in one year to February in the next year when reptiles in the study area are most active. Our study took place over six consecutive field seasons, from Dec 2004 – Feb 2005 (season 1) to Nov 2009 – Feb 2010 (season 6). We surveyed a total of 25 sites, 11 at Hincks and 14 at Pinkawillinie, representing a range of post-fire habitat stages (0-50 yr, Table 2.1). At each reserve, we used two trapping protocols, differing in the number and configuration of traps within a site and the seasons in which they were used. Eleven sites (five at Hincks, six at Pinkawillinie) had 22 pitfall traps arranged in pairs at 40 m intervals along a 400 m transect, with a 20 m drift fence intersecting each trap pair (Driscoll & Henderson 2008). The transects were aligned perpendicular to the angle of the dunes so that they sampled both dune and swale microhabitats. These "transect" sites were surveyed in seasons 1-4 (Table 2.1). Fourteen sites (six at Hincks, eight at Pinkawillinie) had 25 pitfall traps in a 1 ha grid, with five rows of five traps spaced at 25 m intervals, each intersected by a 10 m drift fence (Smith et al. 2012). Each grid straddled a single dune and sampled mainly on deep, sandy soil. These "grid" sites were surveyed in seasons 5-6 (Table 2.1) and were in the same general areas of the reserves as the transect sites. *Triodia* was present at all but one of our sites (P7). Traps at both the transect and grid sites consisted of a 20 litre bucket buried flush with the ground surface. Trapped animals could shelter in a half PVC pipe placed at the bottom of each bucket and covered with a wood block which also acted as a floating refuge in the very rare case of heavy rain. Some trapping sites were located within the same fire boundary. Our statistical models accounted for differences between the two protocols and for repeated sampling within fire boundaries (see *2.3.3 Analysis*).

Table 2.1. We surveyed 25 sites using two trapping protocols over six seasons. Sites represented a range of post-fire habitat stages. Four sites that burnt during the study (I3, I4, P3, P4) were analysed as separate observations before and after the fire.

Location	Site	Protocol	Seasons surveyed	No. trap nights	Last fire
Hincks	I1	transect	1-4	1694	1999
	I2	transect	1-2	770	1999
	I3	transect	1-4	1694	1977/2006
	I4	transect	1-4	1694	1977/2006
	I7	transect	3-4	770	1977
	HIE1	grid	5-6	1400	2006
	HIE2	grid	5-6	1400	2006
	HIM1	grid	5-6	1400	1999
	HIM2	grid	5-6	1400	1999
	HIL6	grid	5-6	1400	1966
	HIL7	grid	5-6	1400	1966
Pinkawillinie	P1	transect	1-4	1694	2001
	P2	transect	1-4	1694	2001
	P3	transect	1-4	1694	1986/2005
	P4	transect	1-4	1694	1986/2005
	P7	transect	3-4	924	1986
	P8	transect	3-4	924	1986
	PE1	grid	5-6	1075	2005
	PE2	grid	5-6	1075	2005
	PM1	grid	5-6	1075	2001
	PM2	grid	5-6	1075	2001
	PL1	grid	5-6	1075	1960
	PL2	grid	5-6	1075	1960
	PL3	grid	5-6	1075	1960
	PL4	grid	5-6	1075	1960

In five of the six seasons, three trapping sessions were conducted. There were only two trapping sessions in season 2. Transect sites were all surveyed for seven nights in each trapping session (21 nights per season, and 14 in season 2). Trapping sessions at the grid sites varied from 5-15 nights (mean = 8), and totaled 18 and 21 nights (season 5), and 38 and 22 nights (season 6) for Hincks and Pinkawillinie, respectively. Traps within each reserve were opened and closed at the same times (Driscoll & Henderson 2008; Smith et al. 2012). Overall, there were 592 traps and 32,246 trap nights in our study (Table 2.1).

While open, traps were checked every morning. All captured reptiles were identified following Wilson and Swan (2010), except *Pogona spp.* which could not be reliably identified in the field. Mitochondrial DNA analysis identified two allopatric *Pogona* clades on the Eyre Peninsula with a boundary between Hincks and Pinkawillinie (J. Melville, Museum Victoria, pers. comm.). Location differences in *Pogona spp.* may therefore represent species differences. At the transect sites all animals were given a unique mark to allow identification upon recapture and only initial captures were included in the analysis. Marks consisted of toe clips for skinks and agamids, fluorescent ventral marks for geckos (Smith et al. 2012) and ventral paint spots for snakes and pygopodids. All marks were permanent except paint spots which would likely rub off between seasons. However, recapture rates of legless reptiles within trapping sessions were low (< 0.2), so between-season recaptures would likely be lower. At the grid sites, unique marks were only given to three species targeted for related studies (*Amphibolurus norrisi* (Agamidae), *Ctenotus atlas* (Scincidae) and *Nephrurus stellatus* (Gekkonidae)). For other species recorded at the grid sites, capture numbers were adjusted using recapture rates for each species (0-0.22, mean = 0.06) from Hincks and Pinkawillinie separately (count - (count x recapture rate)).

Data from all trapping sessions across all seasons were combined for sites that were not burnt during the study, giving a total count for each species at each site that could be standardised for trap effort. The maximum number of years over which data were combined was four. Successional changes in habitat over these time periods would be negligible compared to the time scale of our analysis (50 years) and any subtle changes are likely to have been masked by variable weather conditions during the surveys (Driscoll & Henderson 2008; Driscoll et al. 2012). Data were collected both before and after fires at four sites that burnt during the study (Table 2.1). Unplanned wildfires burnt P3 and P4 in late December 2005, and I4 in early December 2006. A prescribed fire was conducted at I3 in April 2006. To incorporate data from these sites into the analysis, capture records were treated as separate observations before and after the fire. This was justified because reptile community composition (Driscoll & Henderson 2008) and habitat structure (Smith et al. 2012) at our sites are influenced more by fire history than geographic proximity within reserves.

Driscoll et al. (2012) found that increased capture rates immediately after fire of four of our study species (*Ctenotus atlas*, *Diplodactylus calcicolus*, *Lerista distinguenda*, and *Morethia obscura*) reflected increased local movement in the days to weeks after the fire, rather than changes in local abundance. This did not occur in seven other species (Driscoll et al. 2012). All records for the four species that showed increased movement were removed from the trapping sessions that occurred in the same season, and after the fire (the last session in season 2 for P3 and P4 and all of season 3 for I3 and I4). Trap effort was adjusted accordingly for species at sites that had data removed. Excluding the species with increased movement, Driscoll et al. (2012) found no differences in detectability across three post-fire habitat categories (0-2, 5-10, and >20 years) using occupancy models for reptiles captured at our sites. Other studies using pitfall traps for reptiles have similarly found little evidence for habitat related variation in detectability (Schlesinger 2007; Craig et al. 2009; Smith et al. 2012). We therefore assumed that detectability was similar among successional stages and used the number of captures as an index of abundance.

2.3.3 Analysis

For each survey site, time since fire (TSF) was calculated as the average number of years since the most recent fire during the sampling period for that site. We analysed data from 16 reptile species with an equal or greater number of captures than sample site observations ($N = 29$) (Didham et al. 1998). We used generalised linear mixed models to predict the effect of TSF on abundance of these reptile species. To account for variation in trap effort among sites, we used the number of captures per 1000 trap nights as our response variable. To allow for non-linear responses we fitted TSF and its quadratic form (TSF^2) as fixed effects after standardising both of these terms ((x - mean (x)) / standard deviation (x)) (Quinn & Keough 2002). For species with a suitable sample size at both reserves, location was fitted as a fixed effect and we included its interaction with both TSF terms. To account for our grouped sampling design (2-4 sites were sampled within a single fire boundary) we fitted fire (a factor naming individual fire events) as a random effect. We also included survey protocol (transect or grid) as a random effect to account for variance caused by differences in trap configuration and survey years. The models were fitted with a Poisson link function using glmer in the lme4 package (Bates et al. 2011) for R 2.14 (R Development Core Team 2011).

We calculated the dispersion parameter as the sum of squared residuals / n-p-1, where n is the number of observations and p is the number of fixed effects in the model (Zuur et al. 2009). In models where the dispersion parameter was > 1.5 (Zuur et al. 2009), we added an observation level random effect to account for overdispersion (Maindonald & Braun 2010). If TSF^2 was not significant in the resulting model ($P > 0.1$), we removed it and re-fitted the model. We visually examined the residuals of each model to assess normality and homogeneity of variance. If a strong outlying residual was identified, we removed the outlier and re-fitted the model following the above process. To estimate abundance from the final models we used predictSE.mer in the AICcmodavg package (Mazerolle 2011). For comparison with Driscoll and Henderson (2008) and to reduce the risk of Type II errors (Driscoll & Weir 2005) we inferred significant effects of TSF on abundance where $P < 0.1$.

We statistically examined relationships between the fire response of each species and their ecological traits for each location separately. Each species with a significant response to TSF was assigned to a fire category based on its change in abundance. Given the small number of species analysed at each location (Hincks = 11, Pinkawillinie = 9), we grouped fire responses into two general categories. The "Early/Mid" category included species with a linear abundance decrease with increased TSF (early successional) and species with an initial increase followed by a decrease (mid successional). The "Late" category included species with linear increases in abundance with TSF (late successional). For ecological traits, we used our personal observations and published literature (Pianka 1969; Cogger 1974; Abensperg-Traun & Steven 1997; Driscoll & Henderson 2008; Goodyear & Pianka 2008; Wilson & Swan 2010) to classify each species by its activity pattern, shelter type, foraging habitat, and diet (see 2.4 Results). We grouped traits in each category into two factor levels: activity = nocturnal/diurnal, shelter type = burrow/not burrow, foraging habitat = open ground/within vegetation, diet = generalist/specialist. These groupings corresponded to those suggested in previous reports to be important to fire responses in reptiles (Caughley 1985; Friend 1993; Letnic et al. 2004). We then used Fisher's exact tests to investigate relationships between the fire response and ecological trait categories.

2.4 Results

We recorded 4796 individual reptiles from 44 species in seven families (Supporting material 2.8.1) and 16 species had sample sizes suitable for analysis (Table 2.2, Supporting material 2.8.2). Eight species were analysed for both reserves, and eight at one reserve (Table 2.2). We identified significant main effects of TSF (or TSF^2) and/or interactive effects between TSF and location, on the abundance of 13 of the 16 reptile species analysed (Table 2.2, Fig. 2.2a-t). The abundance of three species (*Ctenophorus cristatus*, *Ctenotus euclae*, and *Morethia obscura*) was not significantly affected by TSF (Table 2.2). Of the eight species analysed at both locations, all had significant effects of location, with four captured in higher numbers at Hincks and four with greater abundance at Pinkawillinie (Table 2.2).

The significant response to TSF in five species (*Amphibolurus norrisi*, *Ctenophorus fordi*, *Ctenotus atlas*, *Lucasium damaeum*, *Nephrurus stellatus*) had been reported in previous studies, and these were generally in the same direction (Driscoll & Henderson 2008; Driscoll et al. 2012). However, Driscoll et al. (2012) reported an abundance peak at 5-10 years since fire for *C. fordi* and *N. stellatus*. The current study showed a linear decline with TSF at both locations for *C. fordi* (Fig. 2.2a,b) and at Pinkawillinie for *N. stellatus* (Fig. 2.2l). A model where TSF was log transformed revealed a very early abundance increase in our data for *C. fordi* but that model was not used because of a poor fit to data from most other species (Supporting material 2.8.3). Driscoll and Henderson (2008) reported a late successional response in *C. atlas* at Pinkawillinie, but no response at Hincks. In the current study, *C. atlas* had late-successional response at both locations (Fig. 2.2c,d). One species (*Ctenophorus cristatus*) which had previously been reported to respond to TSF (Driscoll and Henderson 2008) did not show a significant response in analysis of the larger data set used in this study.

Table 2.2 The number of individuals captured for the 16 species analysed and statistics from generalised linear mixed models (GLMM). Significant *P* values ($\alpha = 0.1$) are indicated in bold.

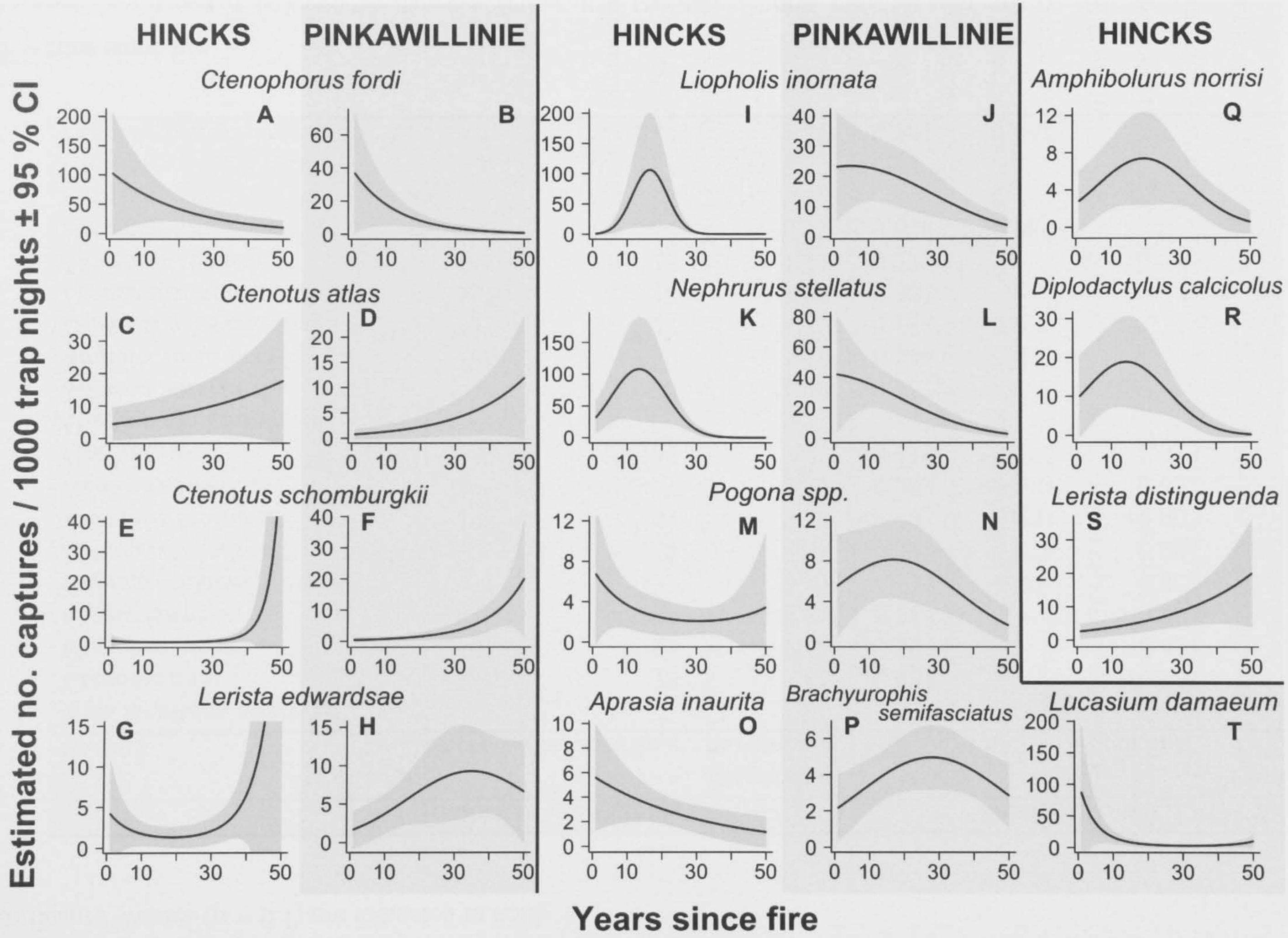
	Number of individuals			**P values from GLMM fixed effects**				
Species	**Hincks**	**Pinkawillinie**	**Dispersion parameter**	**TSF**	**TSF^2**	**Location**	**Location x TSF**	**Location x TSF^2**
Two locations analysed								
Ctenotus atlas	158	78	1.95	**0.056**	-	**<0.001**	0.158	-
Ctenotus euclae	361	42	2.50	0.161	-	**0.001**	0.419	-
Ctenophorus fordi	876	243	4.88	**0.018**	-	**<0.001**	0.256	-
Ctenotus schomburgkii *	32	133	3.97	0.227	**0.076**	**0.023**	0.163	0.135
Lerista edwardsae *	76	128	4.58	0.140	**0.070**	**0.091**	**0.035**	**0.028**
Liopholis inornata *[†]	194	261	3.33	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Nephrurus stellatus	460	377	2.27	**0.003**	**<0.001**	**0.032**	**0.010**	**0.003**
Pogona spp. *	47	108	2.27	0.210	0.370	**0.013**	**0.087**	**0.095**
One location analysed								
Aprasia inaurita *	43	15	1.40	**0.062**	-	-	-	-
Amphibolurus norrisi	83	0	1.19	**0.096**	**0.061**	-	-	-
Diplodactylus calcicolus *	133	22	4.39	0.128	**0.030**	-	-	-
Lerista distinguenda *	117	8	2.87	**0.002**	-	-	-	-
Morethia obscura	45	15	1.41	0.578	-	-	-	-
Brachyurophis semifasciatus *	0	62	0.97	**0.088**	**0.085**	-	-	-
Ctenophorus cristatus	0	163	5.49	0.937	-	-	-	-
Lucasium damaeum	0	224	1.87	**0.001**	**0.003**	-	-	-

TSF = time since fire.

* Response not detected with smaller data sets (Driscoll & Henderson 2008; Driscoll et al. 2012).

[†] One strong outlying residual was removed before re-fitting the model for *L inornata*.

Fig. 2.2 Of 16 reptile species analysed, the capture rate of 13 was significantly affected by time since fire ($P < 0.1$). Some species were analysed at two locations, and others at only one.



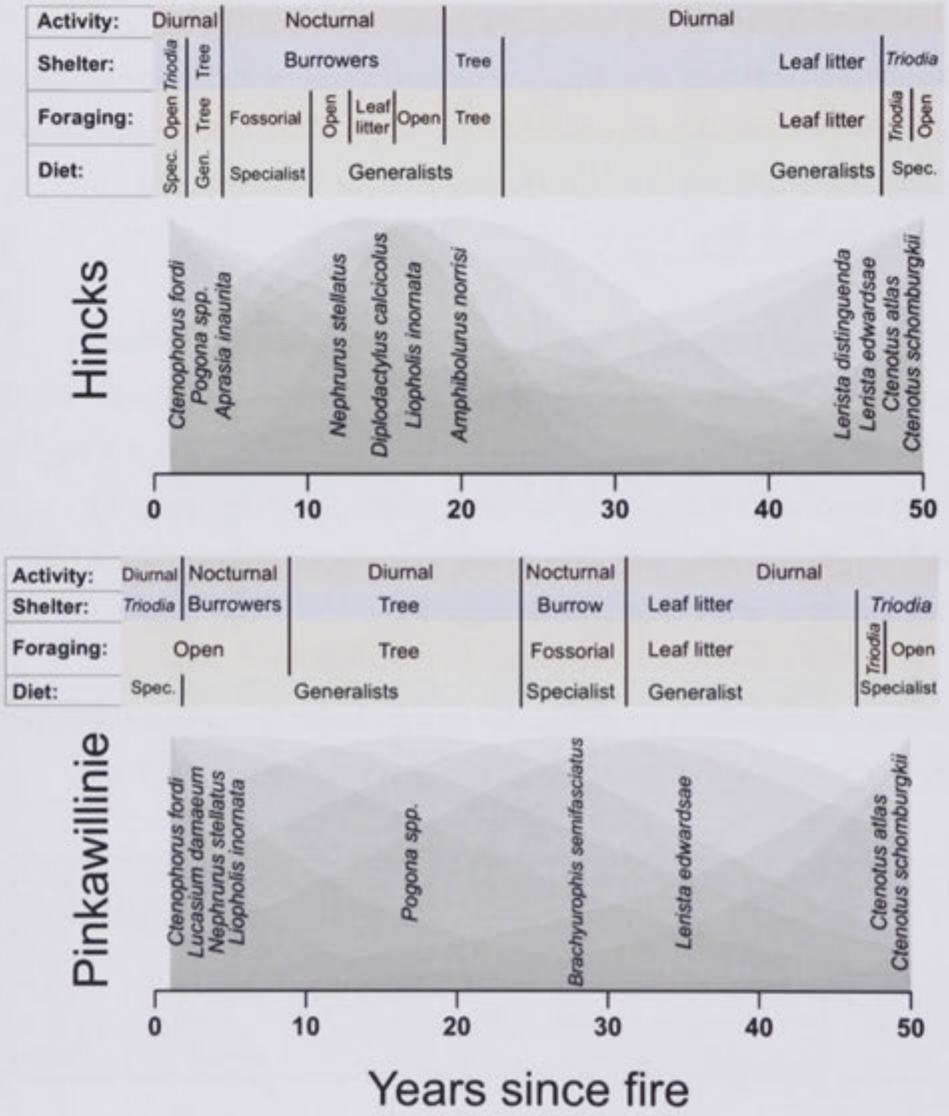
Our analysis revealed significant responses to TSF in an additional eight species that were not found to respond previously (Table 2.2). Of these species, abundance of *Aprasia inaurita* declined linearly with TSF (Fig. 2.2o), while *Ctenotus schomburgkii* (Fig. 2.2e,f) and *Lerista distinguenda* (Fig. 2.2s) had late successional responses. *Brachyurophis semifasciatus* (Fig. 2.2p) and *Diplodactylus calcicolus* (Fig. 2.2r) both had an initial abundance increase with TSF followed by a decline. The response of three other species varied between the two locations. *Liopholis inornata* (Fig. 2.2i,j) had a mid-successional peak at Hincks and an early successional peak at Pinkawillinie, while the opposite response occurred in *Pogona spp.* (Fig. 2.2m,n). Abundance estimates for *Lerista edwardsae* were greatest at 50 and 35 years since fire for Hincks and Pinkawillinie, respectively (Fig. 2.2g,h).

Our analysis of ecological traits (Supporting material 2.8.4) showed a significant relationship ($\alpha = 0.1$) between fire category and shelter type at Pinkawillinie ($P = 0.074$, Table 2.3). No other tests of fire and trait categories were significant (Table 2.3, Fig. 2.3, Supporting material 2.8.4). However, we observed non-significant trends for nocturnal and burrowing reptiles to be early or mid successional, and diurnal and leaf-litter dwelling species to be late successional (Fig. 2.3).

Table 2.3 *P*-values from Fisher's exact tests. We tested whether fire category could be explained by four ecological trait categories (details in Supporting material 2.8.4).

Trait	**Trait categories for analysis**	**Location**	
		Hincks	**Pinkawillinie**
Activity	Nocturnal / Diurnal	0.178	0.124
Shelter type	Burrow / Not burrow	0.184	0.074
Foraging habitat	Open ground / Within vegetation	1.000	0.545
Diet	Generalist / Specialist	0.569	0.545

Fig 2.3 The response and life-history attributes of 13 reptile species that were significantly affected by post-fire succession. The name of each species is indicated at the point where it was most abundant. The grey shading is the mean abundance for each species and is shown to illustrate the variation in fire responses among the reptile community.



2.5 Discussion

Understanding responses to fire in animals is essential for implementing appropriate management, thus we aimed to investigate post-fire succession using a large data set from an Australian reptile community. Our study had two important findings. First, we found eight significant response patterns that were not detected in previous analyses that used substantial subsets of the data from shorter sampling periods. The majority of reptile species for which we had adequate data (13/16) showed a significant abundance response to time since fire in at least one of the two study locations, indicating a high degree of successional specialisation. Our findings highlight a risk that fire management decisions that are based on insufficient data could fail to incorporate the complexity of responses in animal communities, particularly in those taxa which require large effort to accumulate adequate samples. Our second important finding was that habitat use and life history traits did not adequately describe species responses to time since fire. However, we observed some general trends related to shelter site and activity patterns that may not have been statistically significant because of the small number of species available for analysis (Fig. 2.3). A number of refinements are required to build a predictive framework for ecological fire management based on generalised species properties for reptiles, and we discuss these below.

2.5.1 Detecting fire responses in reptiles

A number of studies have found limited effects of post-fire succession on reptile communities (Ford et al. 1999; Lindenmayer et al. 2008; Perry et al. 2009). In mallee ecosystems, two previous studies showed that the abundance of most reptile species did not vary with time since fire (Driscoll & Henderson 2008; Driscoll et al. 2012). Woinarski et al. (2004a) suggested that the survey effort used in many studies is not sufficient to detect fire responses in reptiles. Results from our study support this suggestion because we found eight species with significant responses to time since fire that were not detected in previous studies using smaller subsets of the same data (Driscoll & Henderson 2008; Driscoll et al. 2012). It is therefore essential to recognise the limitations of studies with short term or low intensity sampling when making fire management recommendations. Even in the current study, 28 of the 44 reptile species captured provided inadequate data to detect any fire response trends. Driscoll et al. (2012) used a more conservative test of significance ($\alpha = 0.05$ and adjustment for multiple tests) than used by Driscoll and Henderson (2008) and in the current study. Using statistical approaches that minimise Type II errors (e.g. Driscoll and Weir 2005) may be important when examining vertebrate responses to fire. The risk of Type I errors is probably lower as only one species (*Ctenophorus cristatus*) that was previously reported to respond to fire (Driscoll & Henderson 2008) did not have a significant response in this study.

A major strength of two previous fire studies on mallee reptiles was regional replication across five different conservation reserves (Driscoll & Henderson 2008; Driscoll et al. 2012). In our study, we sacrificed some of this replication for more intensive sampling at only two reserves. Our increased sample size and sites at a greater number of post-fire stages gave us the power to detect successional responses that were previously undetected in eight reptile species. However, reptile distributions can vary greatly across regions as can their response to succession (Driscoll & Henderson 2008). This variation is one of the reasons that such immense survey effort is needed to detect fire responses in reptiles (Woinarski et al. 2004a). It is therefore important to achieve a balance between sampling intensity and spatial replication so that studies can identify potential regional variation in species responses to fire.

In our study we were restricted by available fire records (DENR 2011) to examining succession up to only 50 years after fire. Mallee can remain unburnt for well over a century (Clarke et al. 2010). The habitat features that develop beyond the temporal scope of our study, and indeed many studies, are important for many animal species (Haslem et al. 2011; Kelly et al. 2011). Studies which define successional trajectories of reptiles beyond 50 years are needed for developing both succession theory and fire management protocols.

2.5.2 Can we predict succession of mallee reptile communities?

Previous studies suggested that traits related to daily activity cycles, shelter sites, foraging habitat, and diet could be used to predict post-fire succession in reptile communities (Caughley 1985; Friend 1993; Letnic et al. 2004). In our study, only shelter use at Pinkawillinie explained variation in reptile fire responses, as all species in the "late" fire category were non-burrowers. In addition to this result, we observed some non-significant relationships between fire responses and traits related to shelter and activity (Fig. 2.3). The limited number of species with enough data to be analysed at each location (Hincks = 11, Pinkawillinie = 9) may have been too small for statistical inference, or the variation in these relationships between locations could have masked a significant result. However, we discuss these patterns below.

At Hincks burrowing species all peaked in abundance between one and 17 years after fire. At Pinkawillinie all burrowers peaked within five years after fire (except *Brachyurophis semifasciatus* which peaked at 28 yr), explaining the significant shelter effect at this location. All burrowing species in our study were also nocturnal. *Liopholis inornata* was the only skink with an early successional abundance peak and this species is, unusually for skinks, reported to be crepuscular to nocturnal (Wilson & Swan 2010). Letnic et al. (2004) suggested that shelter from above ground vegetation is less important for nocturnal than diurnal species, meaning nocturnal species can more swiftly recolonise after fire, and our findings support this. Furthermore, nocturnal reptiles rely on heat transfer from substrates (Schlesinger et al. 1997) which are likely to be warmer in recently burnt areas (Hossack et al. 2009). Caughley (1985) and Friend (1993) predicted early successional responses to fire for burrowers that forage on open ground. In our study, some burrowing species were fossorial (*Brachyurophis semifasciatus* and *Aprasia inaurita*) or leaf-litter (*Diplodactylus calcicolus*) foragers and our results did not support suggestions that fire responses are related to foraging habitat (Caughley 1985; Friend 1993). Burrowing species may be supported by habitats with up to 28 years since fire, longer than suggested by Caughley (1985), but the response varies among species. The decline of these species with time since fire could be caused by several factors including increased competition from later successional species or increased predation (Hawlena et al. 2010), reduced movement and dispersal (Templeton et al. 2011), or an unfavourable thermal environment (Hossack et al. 2009) and its related effects on reproduction (Smith et al. 2012).

The four late successional species in our study were either leaf-litter dwellers (*Lerista distinguenda*, *Lerista edwardsae*) or *Triodia* dwellers (*Ctenotus atlas*, *Ctenotus schomburgkii*) and all were diurnal skinks. Caughley (1985) suggested that the fire response of leaf-litter specialists follows the build-up of their habitat which takes approximately 20 years in mallee habitats (Haslem et al. 2011). Our findings support this prediction for leaf-litter dwellers. However, we did not find any evidence to support Caughley's (1985) prediction that *Triodia* specialist reptiles peak in abundance six years after fire then remain stable. This is probably because the response of *Triodia* itself does not always follow this pattern. At our study sites *Triodia* has a linear increase with time since fire (A.L. Smith, unpublished data), and is probably affected by variation in grazing and rainfall patterns that interact with fire regimes (Driscoll et al. 2012). In other mallee regions of Australia, *Triodia* continues to increase in density for 30 years after fire (Haslem et al. 2011). The late successional response of *Triodia* specialists *C. atlas* and *C. schomburgkii* may therefore reflect the change in their habitat plant at our study sites, consistent with a habitat accommodation model of succession. *Ctenophorus fordi* has been described as entirely dependent on *Triodia* (Cogger 1974) so its sharp decline with time since fire at both locations is not consistent with a habitat accommodation model. It is possible that *C. fordi* can readily supplement *Triodia* habitat in early post-fire stages by using burrows and other habitat features (Driscoll & Henderson 2008). The decline with time since fire despite the availability of suitable habitat could be related to increased competition from late successional species (Sarà et al. 2006).

Caughley (1985) gave no prediction for semi-arboreal species which, in our study, were captured more commonly in either the early or mid successional stages. The mid successional response we found for *Amphibolurus norrisi* at Hincks was also found by Driscoll and Henderson (2008) and they reported a late successional response at another reserve (Heggaton) that we did not survey. This interaction could not be explained by time since fire (Driscoll & Henderson 2008). In the current study, the semi-arboreal *Pogona spp.* also showed a variable response among reserves. At Hincks it was most common in the recently burnt habitat, while at Pinkawillinie it had a mid successional response. These contrasting fire responses might represent ecological differences between the two *Pogona* clades, or they might represent an interactive effect of fire with some other change in the ecosystem. Fire frequency and fire return interval can have substantial effects on vegetation structure (Pausas & Lloret 2007; Vilà-Cabrera et al. 2008), that may affect important habitat attributes for semi-arboreal reptiles, such as shrub density, or the density of standing dead sticks. Inclusion of more comprehensive fire regime characteristics into future studies may help explain regional variation in fire-responses within reptile species.

In summary, we found that nocturnal burrowers tended (non-significantly) to be early or mid successional, and diurnal leaf-litter dwellers tended (non-significantly) to be late successional, consistent with a habitat accommodation model (Caughley 1985; Friend 1993; Letnic et al. 2004). We did not observe any relationships between fire responses and foraging habitat or diet, and the response for *Triodia* specialists in our study did not follow previous predictions (Caughley 1985). Our findings are based on general trends as we did not find statistically significant relationships between fire responses and traits.

Unfortunately, detailed ecological information on most reptile species is scarce. Traits we could not examine included reproduction, longevity and dispersal, but these are probably of great importance in determining fire responses (Templeton et al. 2011; Smith et al. 2012). To build predictive models for fire responses in animal communities we need (i) a better understanding of species-level ecology (e.g. Templeton et al. 2011), (ii) models that include a wider range of demographic and dispersal traits (e.g. Langlands et al. 2011), (iii) detailed measures of habitat structure and other fire regime characteristics (intensity, frequency, and severity) in addition to simple measures of time since fire (e.g. Di Stefano et al. 2011), (iv) incorporation of potentially interacting factors including climatic variables and grazing (e.g. Kirkpatrick et al. 2011), and (v) landscapes with a broad range of time since fire (e.g. Kelly et al. 2011) and fire frequency (e.g. Westgate et al. 2012) patterns that can be replicated at a regional spatial scale.

2.5.3 Fire management for fauna conservation

Observations of contrasting responses to fire within animal communities often lead to the conclusion that a fire-mosaic, i.e. a successionally heterogeneous landscape, should be maintained in an ecosystem (e.g. Masters 1996; Briani et al. 2004). However, defining the appropriate spatial and temporal scales of fire mosaics for fauna has only rarely been attempted (e.g. Bradstock et al. 2005).

For reptiles, management that increases early and more open successional habitats is often suggested to be beneficial because reptiles rely on basking opportunities to regulate their body temperature (e.g. Greenberg et al. 1994; Pike et al. 2011(2011)). Bury (2004) claimed that "most reptiles are adapted to open terrain, so fire usually improves their habitat". It is important that statements like this are based on adequate data, otherwise the resulting management recommendations could be harmful to some species. In our study, we found four skink species that were most common in long unburnt habitats (*Ctentous atlas*, *C. schomburgkii*, *Lerista edwardsae*, and *L. distinguenda*). In previous studies with smaller sample sizes, only one of these responses was detected (*C. atlas*), while a higher proportion (44%) of early and medium successional responses were detected previously. Fire studies on reptiles might be biased towards detecting early successional responses. Driscoll et al. (2012) gave direct evidence for this in the mallee ecosystem. They captured several reptile species immediately after fire that had otherwise only been captured in very low numbers over four years, or not at all. A suite of reptile species probably specialise on late-successional habitats, but go unstudied because they have behavioural traits that make them hard to detect (Driscoll et al. 2012).

Our results showed that the majority of common reptiles specialise on a particular post-fire stage, and may become threatened if fire is not managed appropriately. Our data support the prescription that extreme fire regimes, including widespread burning or long-term fire suppression, should be avoided. Quantifying appropriate spatial and temporal scales of fire mosaics for fauna is clearly an immediate research priority (Clarke 2008). The use of spatially explicit simulation models is one way to achieve this (Turner et al. 1994; Bradstock et al. 2005) and the study of species-level ecology should continue so that these models can be parameterised (Driscoll et al. 2010b). In the meantime, results from short-term fire studies of vertebrates should be interpreted with the knowledge that many responses to fire may not have been detected. To conserve biodiversity, fire management decisions should be based on quantitative studies of many species within a community.

2.6 Acknowledgements

Field work for this project was completed with the enormous effort of over 100 volunteers. Ian Sellar and Samantha Blight coordinated field work in seasons 2 and 4, respectively. We thank members of the South Australian Department of Environment and Natural Resources (DENR) at Pt. Lincoln, particularly Joe Tilley for logistical support in the field. Mark Hutchinson provided valuable help with reptile identification. Thanks to Hwan-Jin Yoon and Wade Blanchard for statistical advice and to Martin Westgate for help with automating the analysis. This study was supported by funds from the Australian Research Council, The Australian National University, DENR, Flinders University, and the Australia and Pacific Science Foundation. DD was supported by funding from the Australian Government's National Environmental Research Program and the Australian Research Council Centre of Excellence for Environmental Decisions. We worked under animal ethics permits from Flinders University (E194 and E256) and research permits from DENR (Q24788 and S25589).

2.7 References

Abensperg-Traun M. and Steven D. (1997). Ant- and termite-eating in Australian mammals and lizards: a comparison. *Australian Journal of Ecology* 22: 9-17.

Andersen A.N., Woinarski J.C.Z. and Parr C.L. (2012). Savanna burning for biodiversity: fire management for faunal conservation in Australian tropical savannas. *Austral Ecology*: DOI 10.1111/j.1442-9993.2011.02334.x.

Bates D., Maechler M. and Bolker B. (2011). *lme4: linear mixed-effects models using S4 classes.* R package, version 0.999375-40. http://lme4.r-forge.r-project.org/ (accessed September 2011).

Betts M.G., Hagar J.C., Rivers J.W., Alexander J.D., McGarigal K. and McComb B.C. (2010). Thresholds in forest bird occurrence as a function of the amount of early-seral broadleaf forest at landscape scales. *Ecological Applications* 20: 2116-2130.

Bradstock R.A., Bedward M., Gill A.M. and Cohn J.S. (2005). Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. *Wildlife Research* 32: 409-423.

Bradstock R.A. and Cohn J.S. (2002). Fire regimes and biodiversity in semi-arid mallee ecosystems. In: *Flammable Australia: the fire regimes and biodiversity of a continent.* (eds. Bradstock RA, Williams JE, Gill AM). Cambridge University Press, Cambridge.

Briani D.C., Palma A.R.T., Vieira E.M. and Henriques R.P.B. (2004). Post-fire succession of small mammals in the Cerrado of central Brazil. *Biodiversity and Conservation* 13: 1023-1037.

Brisson J.A., Strasburg J.L. and Templeton A.R. (2003). Impact of fire management on the ecology of collared lizard (*Crotaphytus collaris*) populations on the Ozark Plateau. *Animal Conservation* 6: 247-254.

Bury R.B. (2004). Wildfire, fuel reduction, and herpetofaunas across diverse landscape mosaics in northwestern forests. *Conservation Biology* 18: 968-975.

Caughley J. (1985). Effect of fire on the reptile fauna of mallee. In: *Biology of Australasian frogs and reptiles.* (eds. Grigg G, Shine R, Ehmann H), pp. 31-34. Royal Zoological Society of NSW and Surrey Beatty & Sons., Chipping Norton, NSW.

Clarke M.F. (2008). Catering for the needs of fauna in fire management: science or just wishful thinking? *Wildlife Research* 35: 385-394.

Clarke M.F., Avitabile S.C., Brown L., Callister K.E., Haslem A., Holland G.J., Kelly L.T., Kenny S.A., Nimmo D.G., Spence-Bailey L.M., Taylor R.S., Watson S.J. and Bennett A.F. (2010). Ageing mallee eucalypt vegetation after fire: insights for successional trajectories in semi-arid mallee ecosystems. *Australian Journal of Botany* 58: 363-372.

Cogger H.G. (1974). Thermal relations of the mallee dragon *Amphibolurus fordi* (Lacertilia: Agamidae). *Australian Journal of Zoology* 22: 319-339.

Craig M.D., Grigg A.H., Garkaklis M.J., Hobbs R.J., Grant C.D., Fleming P.A. and Hardy G.E.S.J. (2009). Does habitat structure influence capture probabilities? A study of reptiles in a eucalypt forest. *Wildlife Research* 36: 509-515.

DENR (2011). *NatureMaps* Department of Environment and Natural Resources. http://www.naturemaps.sa.gov.au/ (accessed September 2011).

Di Stefano J., Owen L., Morris R., Duff T. and York A. (2011). Fire, landscape change and models of small mammal habitat suitability at multiple spatial scales. *Austral Ecology* 36: 638-649.

Didham R.K., Hammond P.M., Lawton J.H., Eggleton P. and Stork N.E. (1998). Beetle species responses to tropical forest fragmentation. *Ecological Monographs* 68: 295-323.

Doak D.F., Gross K. and Morris W.F. (2005). Understanding and predicting the effects of sparse data on demographic analyses. *Ecology* 86: 1154-1163.

Driscoll D.A. and Henderson M.K. (2008). How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model. *Biological Conservation* 141: 460-471.

Driscoll D.A., Lindenmayer D.B., Bennett A.F., Bode M., Bradstock R.A., Cary G.J., Clarke M.F., Dexter N., Fensham R., Friend G., Gill A.M., James S., Kay G., Keith D.A., MacGregor C., Possingham H.P., Russel-Smith J., Salt D., Watson J.E.M., Williams D. and York A. (2010a). Resolving conflicts in fire management using decision theory: asset-protection versus biodiversity conservation. *Conservation Letters* 3: 215-223.

Driscoll D.A., Lindenmayer D.B., Bennett A.F., Bode M., Bradstock R.A., Cary G.J., Clarke M.F., Dexter N., Fensham R., Friend G., Gill A.M., James S., Kay G., Keith D.A., MacGregor C., Russell-Smith J., Salt D., Watson J.E.M., Williams R.J. and York A. (2010b). Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation* 143: 1928-1939.

Driscoll D.A., Smith A.L., Blight S.R. and Maindonald J. (2012). Reptile responses to fire and the risk of post-disturbance sampling bias. *Biodiversity and Conservation*: DOI 10.1007/s10531-10012-10267-10535.

Driscoll D.A. and Weir T. (2005). Beetle responses to habitat fragmentation depend on ecological traits, habitat condition, and remnant size. *Conservation Biology* 19: 182-194.

Ford W.M., Menzel M.A., McGill D.W., Laerm J. and McCay T.S. (1999). Effects of a community restoration fire on small mammals and herpetofauna in the southern Appalachians. *Forest Ecology and Management* 114: 233-243.

Friend G.R. (1993). Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: a review. *Biological Conservation* 65: 99-114.

Goodyear S.E. and Pianka E.R. (2008). Sympatric ecology of five species of fossorial snakes (Elapidae) in Western Australia. *Journal of Herpetology* 42: 279-285.

Greenberg C.H., Neary D.G. and Harris L.D. (1994). Effect of high-intensity wildfire and silvicultural treatments on reptile communities in sand-pine scrub. *Conservation Biology* 8: 1047-1057.

Gregory N.C., Sensenig R.L. and Wilcove D.S. (2010). Effects of controlled fire and livestock grazing on bird communities in east African savannas. *Conservation Biology* 24: 1606-1616.

Haslem A., Kelly L.T., Nimmo D.G., Watson S.J., Kenny S.A., Taylor R.S., Avitabile S.C., Callister K.E., Spence-Bailey L.M., Clarke M.F. and Bennett A.F. (2011). Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. *Journal of Applied Ecology* 48: 247-256.

Hawlena D., Saltz D., Abramsky Z. and Bouskila A. (2010). Ecological trap for desert lizards caused by anthropogenic changes in habitat structure that favor predator activity. *Conservation Biology* 24: 803-809.

Hossack B.R., Eby L.A., Guscio C.G. and Corn P.S. (2009). Thermal characteristics of amphibian microhabitats in a fire-disturbed landscape. *Forest Ecology and Management* 258: 1414-1421.

Kelly L.T., Nimmo D.G., Spence-Bailey L.M., Haslem A., Watson S.J., Clarke M.F. and Bennett A.F. (2011). Influence of fire history on small mammal distributions: insights from a 100-year post-fire chronosequence. *Diversity and Distributions* 17: 462-473.

Kirkpatrick J.B., Marsden-Smedley J.B. and Leonard S.W.J. (2011). Influence of grazing and vegetation type on post-fire flammability. *Journal of Applied Ecology* 48: 642-649.

Langlands P.R., Brennan K.E.C., Framenau V.W. and Main B.Y. (2011). Predicting the post-fire responses of animal assemblages: testing a trait-based approach using spiders. *Journal of Animal Ecology* 80: 558-568.

Letnic M., Dickman C.R., Tischler M.K., Tamayo B. and Beh C.-L. (2004). The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *Journal of Arid Environments* 59: 85-114.

Lindenmayer D.B., Wood J.T., MacGregor C., Michael D.R., Cunningham R.B., Crane M., Montague-Drake R., Brown D., Muntz R. and Driscoll D.A. (2008). How predictable are reptile responses to wildfire? *Oikos* 117: 1086-1097.

Lyet A., Cheylan M., Prodon R. and Besnard A. (2009). Prescribed fire and conservation of a threatened mountain grassland specialist: a capture-recapture study on the Orsini's viper in the French alps. *Animal Conservation* 12: 238-248.

Maindonald J.H. and Braun W.J. (2010). *Data analysis and graphics using R: an example-based approach*, 3rd edn., Cambridge University Press.

Manley P.N., Zielinski W.J., Schlesinger M.D. and Mori S.R. (2004). Evaluation of a multiple-species approach to monitoring species at the ecoregional scale. *Ecological Applications* 14: 296-310.

Masters P. (1996). The effects of fire-driven succession on reptiles in spinifex grasslands at Uluru National Park, Northern Territory. *Wildlife Research* 23: 39-48.

Mazerolle M.J. (2011). *AICcmodavg.* R package, version 1.2. http://cran.r-project.org/web/packages/AICcmodavg/index.html (accessed September 2011).

Parr C.L. and Andersen A.N. (2006). Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Conservation Biology* 20: 1610-1619.

Pausas J.G. and Lloret F. (2007). Spatial and temporal patterns of plant functional types under simulated fire regimes. *International Journal of Wildland Fire* 16: 484-492.

Perry R.W., Rudolph D.C. and Thill R.E. (2009). Reptile and amphibian responses to restoration of fire-maintained pine woodlands. *Restoration Ecology* 17: 917-927.

Pianka E.R. (1969). Sympatry of desert lizards (*Ctenotus*) in Western Australia. *Ecology* 50: 1012-1030.

Pike D.A., Webb J.K. and Shine R. (2011). Removing forest canopy cover restores a reptile assemblage. *Ecological Applications* 21: 274-280.

Pons P. and Clavero M. (2010). Bird responses to fire severity and time since fire in managed mountain rangelands. *Animal Conservation* 13: 294-305.

Quinn G.P. and Keough M.J. (2002). *Experimental Design and Data Analysis for Biologists.* Cambridge University Press, Cambridge.

R Development Core Team (2011). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Robinson A.C. and Heard M.B. (1985). National Parks. In: *Natural history of Eyre Peninsula.* (eds. Twidale CR, Tyler MJ, Davies M). Royal Society of South Australia, Adelaide, SA.

Sarà M., Bellia E. and Milazzo A. (2006). Fire disturbance disrupts co-occurrence patterns of terrestrial vertebrates in Mediterranean woodlands. *Journal of Biogeography* 33: 843-852.

Schlesinger C.A. (2007). Does vegetation cover affect the rate of capture of ground-active lizards in pitfall traps? *Wildlife Research* 34: 359-365.

Schlesinger C.A., Noble J.C. and Weir T. (1997). Fire studies in mallee (*Eucalyptus spp.*) communities of western New South Wales: reptile and beetle populations in sites of differing fire history. *Rangeland Journal* 19: 190-205.

Smith A.L., Bull C.M. and Driscoll D.A. (2012). Post-fire succession affects abundance and survival but not detectability in a knob-tailed gecko. *Biological Conservation* 145: 139-147.

Specht R.L. (1972). *The Vegetation of South Australia.* AB James, Government Printer, Adelaide, SA.

Templeton A.R., Brazeal H. and Neuwald J.L. (2011). The transition from isolated patches to a metapopulation in the eastern collared lizard in response to prescribed fires. *Ecology* 92: 1736-1747.

Turner M.G., Wu Y., Wallace L.L., Romme W.H. and Brenkert A. (1994). Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. *Ecological Applications* 4: 472-496.

Twidale C.R. and Campbell E.M. (1985). The form of the land surface. In: *Natural history of Eyre Peninsula.* (eds. Twidale CR, Tyler MJ, Davies M). Royal Society of South Australia, Adelaide, SA.

VBRC (2010). Fire preparation, response and recovery. Final Report, Volume II. http://www.royalcommission.vic.gov.au/Commission-Reports/Final-Report.

Vilà-Cabrera A., Saura-Mas S. and Lloret F. (2008). Effects of fire frequency on species composition in a Mediterranean shrubland. *Écoscience* 15: 519-528.

Westgate M.J., Driscoll D.A. and Lindenmayer D.B. (2012). Can the intermediate disturbance hypothesis and information on species traits predict anuran responses to fire? *Oikos*: DOI 10.1111/j.1600-0706.2011.19863.x.

Wilson S. and Swan G. (2010). *A Complete Guide to Reptiles of Australia*, 3 edn. New Holland, Sydney.

Woinarski J.C.Z., Armstrong M., Price O., McCartney J., Griffiths A.D. and Fisher A. (2004a). The terrestrial vertebrate fauna of Litchfield National Park, Northern Territory: monitoring over a 6-year period and response to fire history. *Wildlife Research* 31: 587-596.

Woinarski J.C.Z., Legge S., Fitzsimons J.A., Traill B.J., Burbidge A.A., Fisher A., Firth R.S.C., Gordon I.J., Griffiths A.D., Johnson C.N., McKenzie N.L., Palmer C., Radford I., Rankmore B., Ritchie E.G., Ward S. and Ziembicki M. (2011). The disappearing mammal fauna of northern Australia: context, cause, and response. *Conservation Letters* 4: 192-201.

Woinarski J.C.Z., Risler J. and Kean L. (2004b). Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical *Eucalyptus* open forest, Northern Territory, Australia. *Austral Ecology* 29: 156-176.

Zuur A.F., Ieno E.N., Walker N.J., Saveliev A.A. and Smith G.M. (2009). *Mixed effects models and extensions in ecology with R.* Springer, New York.

2.8 Supporting material

2.8.1 Capture information

Table S2.1 Total number of each of the 44 species in seven families captured during the study. The asterisk (*) indicates the 16 species with sufficient captures for analysis. Footnotes refer to species allocated different names in previous reports (Driscoll & Henderson 2008; Driscoll et al. 2012).

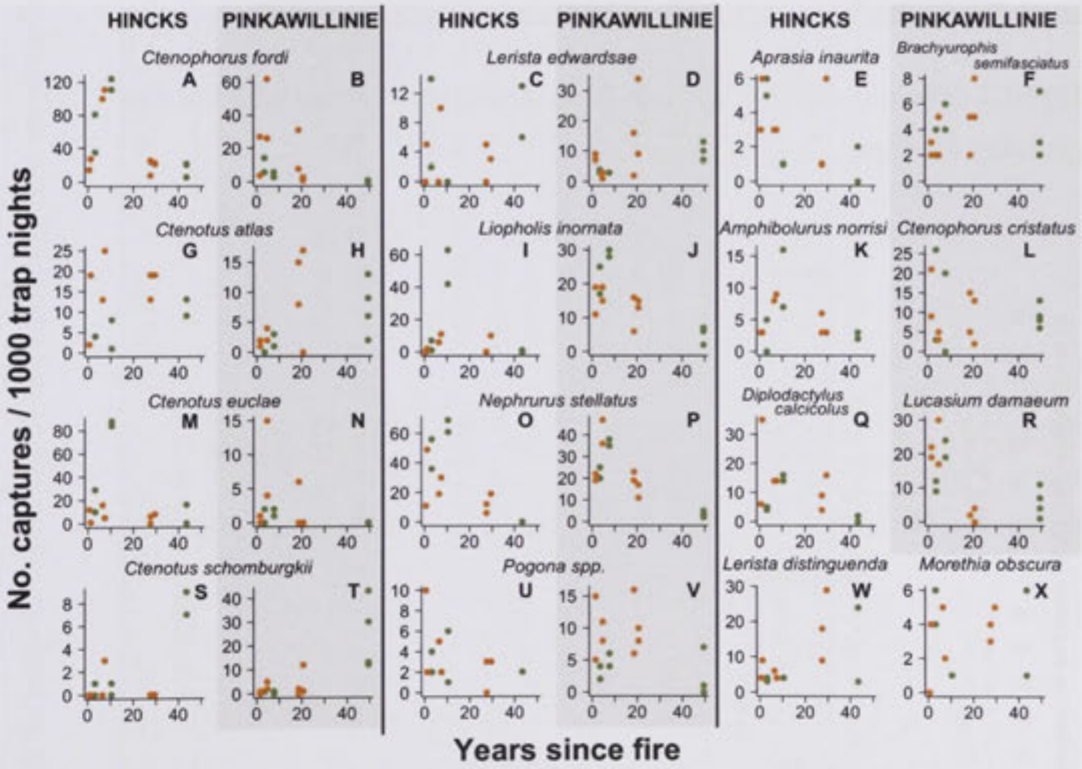
Family	Species	Hincks	Pinkawillinie	Total
Agamidae	*Amphibolurus norrisi* *	83	0	83
	Ctenophorus cristatus *	0	163	163
	Ctenophorus fordi *	876	243	1119
	Moloch horridus	0	12	12
	Pogona spp. *	47	108	155
	Tympanocryptis lineata	1	0	1
Elapidae	*Acanthophis antarcticus*	2	0	2
	Brachyurophis semifasciatus *	0	62	62
	Parasuta spectabilis	3	3	6
	Simoselaps bertholdi	0	17	17
Gekkonidae	*Diplodactylus calcicolus* *[1]	133	22	155
	Gehyra variegata	0	17	17
	Lucasium damaeum *[2]	0	224	224
	Nephrurus stellatus *	460	377	837
	Strophurus assimilis	0	19	19
Pygopodidae	*Aprasia inaurita* *	43	15	58
	Delma australis	7	9	16
	Delma butleri	9	1	10
	Delma fraseri	0	4	4
	Lialis burtonis	4	0	4
	Pygopus lepidopodus	2	2	4
Scincidae	*Cryptoblepharus australis*	0	1	1
	Ctenotus atlas *	158	78	236
	Ctenotus euclae *	361	42	403
	Ctenotus leae	1	9	10
	Ctenotus robustus	0	1	1
	Ctenotus schomburgkii *	32	133	165
	Cyclodomorphus melanops	8	2	10
	Hemiergis peronii	18	0	18
	Lerista distinguenda *	117	8	125
	Lerista dorsalis	20	3	23
	Lerista edwardsae *	76	128	204
	Lerista taeniata	0	25	25
	Liopholis inornata *[3]	194	261	455
	Liopholis multiscutata	3	0	3
	Menetia greyii	1	7	8
	Morethia adelaidensis	0	4	4
	Morethia boulengeri	0	3	3

Family	Species	Hincks	Pinkawillinie	Total
	Morethia butleri	0	4	4
	Morethia obscura *	47	15	62
	Tiliqua occipitalis	2	0	2
Typhlopidae	*Ramphotyphlops bicolor*[4]	20	8	28
	Ramphotyphlops bituberculatus	15	15	30
Varanidae	*Varanus gouldii*	0	8	8
Total		**2743**	**2053**	**4796**

Names given in previous reports: [1] *Diplodactylus granariensis*; [2] *Diplodactylus damaeus*; [3] *Egernia inornata*; [4] *Ramphotyphlops australis*.

2.8.2 Raw data

Fig. S2.1 The number of captures at each site of the 16 species analysed in this study. Orange points are transect sites and green points are grid sites.



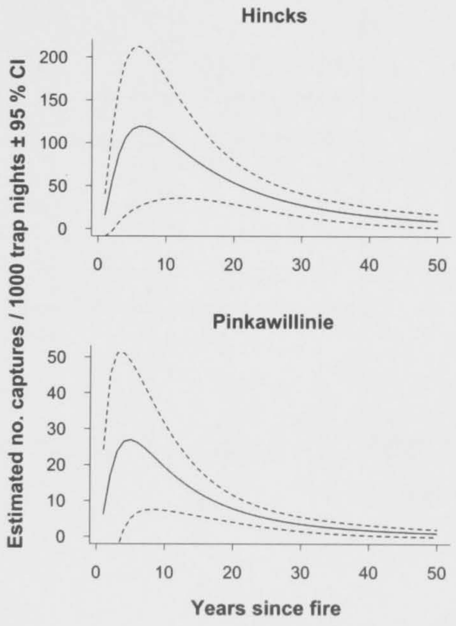
2.8.3 Abundance in Ctenophorus fordi

A model with log-transformed time since fire (TSF) and TSF^2 revealed a very early increase after fire for *Ctenophorus fordi* (Table S2.2, Fig. S2.2). We did not use this as the final model in the analysis log transformation did not provide a good fit for most other species.

Table S2.2 Results from a model for *Ctenophorus fordi* with log-transformed TSF. Three random effects were included: "fire", "protocol" and an observation-level effect to account for overdispersion (dispersion parameter = 4.52) (see *2.3.3 Analysis*).

Parameter	Estimate	SE	z value	Pr(>|z|)
(Intercept)	3.556	0.211	16.835	<0.001
log(TSF)	1.947	0.592	3.291	0.001
location	-1.922	0.319	-6.024	<0.001
log(TSF)^2	-2.577	0.658	-3.915	<0.001
log(TSF):location	-0.274	1.219	-0.225	0.822
log(TSF)^2:location	-0.029	1.239	-0.023	0.982

Fig S2.2 *Ctenophorus fordi* increases in abundance very quickly after fire then gradually declines.



2.8.4 Ecological traits

Table S2.3 The time since fire at which each species was most common (peak abundance). Responses were simplified into two fire categories ("Early/Mid" and "Late") for analysis. Reptile family and ecological traits are given for each species.

Species	**Peak abundance**	**Fire category**	**Family**	**Activity**	**Shelter type**	**Foraging habitat**	**Diet***
Aprasia inaurita	1/-	Early/Mid	Pygopodidae	Nocturnal	Burrow	Fossorial	Ant eggs/larvae (S)
Lucasium damaeum	-/1	Early/Mid	Gekkonidae	Nocturnal	Burrow	Open surface	Arthropods (G)
Ctenophorus fordi	1/1	Early/Mid	Agamidae	Diurnal	*Triodia*	Open surface	Mainly ants (S)
Nephrurus stellatus	13/1	Early/Mid	Gekkonidae	Nocturnal	Burrow	Open surface	Arthropods (G)
Pogona spp.	1/17	Early/Mid	Agamidae	Diurnal	Trees/stumps	Trees/surface	Omnivorous (G)
Liopholis inornata	17/5	Early/Mid	Scincidae	Crepuscular / nocturnal	Burrow	Open surface	Omnivorous (G)
Diplodactylus calcicolus	14/-	Early/Mid	Gekkonidae	Nocturnal	Burrow	Leaf-litter	Arthropods (G)
Amphibolurus norrisi	20/-	Early/Mid	Agamidae	Diurnal	Trees/leaf litter	Trees/surface	Arthropods (G)
Brachyurophis semifasciatus	-/28	Early/Mid	Elapidae	Nocturnal	Burrow	Fossorial	Lizard eggs (S)
Lerista edwardsae[†]	50/35	Late	Scincidae	Diurnal	Leaf-litter	Fossorial/leaf litter	Arthropods (G)
Lerista distinguenda	50/-	Late	Scincidae	Diurnal	Leaf-litter	Leaf-litter	Arthropods (G)
Ctenotus atlas	50/50	Late	Scincidae	Diurnal	*Triodia*	Edges of *Triodia*	Mainly termites (S)
Ctenotus schomburgkii	50/50	Late	Scincidae	Diurnal	*Triodia*	Open surface	Mainly termites (S)
Ctenophorus cristatus	No response	No response	Agamidae	Diurnal	Burrow/logs	Open surface	Arthropods (G)
Ctenotus euclae	No response	No response	Scincidae	Diurnal	Burrow	Open surface	Arthropods (G)
Morethia obscura	No response	No response	Scincidae	Diurnal	Leaf-litter	Leaf-litter	Arthropods (G)

[†] At Pinkawillinie *L. edwardsae* declined slightly after 35 years, but the confidence interval after this point was very wide, so we classified it as "Late" for both locations.

* G = generalist, S = specialist.

Chapter 3

Wildfire-induced mortality of Australian reptiles

Short Communication

Co-authors:
Brendon Meulders
C. Michael Bull
Don A. Driscoll

A summer wildfire in Pinkawillinie Conservation Park left little in the way of shelter for animals relying on above ground vegetation (Photo: A.L. Smith, taken January 2006).

3.1 Abstract

Knowledge of fire-induced mortality in vertebrates is needed to understand population dynamics following fire, and traits that make species susceptible to fire. However, accounts of fire-induced mortality are rare, particularly for Australian reptiles. We surveyed a mallee woodland in southern Australia, 32 days after a severe summer wildfire. Six individual reptiles from six species were found dead (*Acanthophis antarcticus*, *Ctenotus atlas*, *Delma petersoni*, *Demansia reticulata cupreiceps*, *Moloch horridus*, and *Pygopus lepidopodus*) which may have been killed directly by the fire, or may have died soon afterwards. The records included nocturnal and diurnal reptiles, and slow and fast moving species. However, they were all non-burrowing species that shelter in low vegetation and leaf litter. Testing relationships between ecological traits and fire-induced mortality is an important focus for future research.

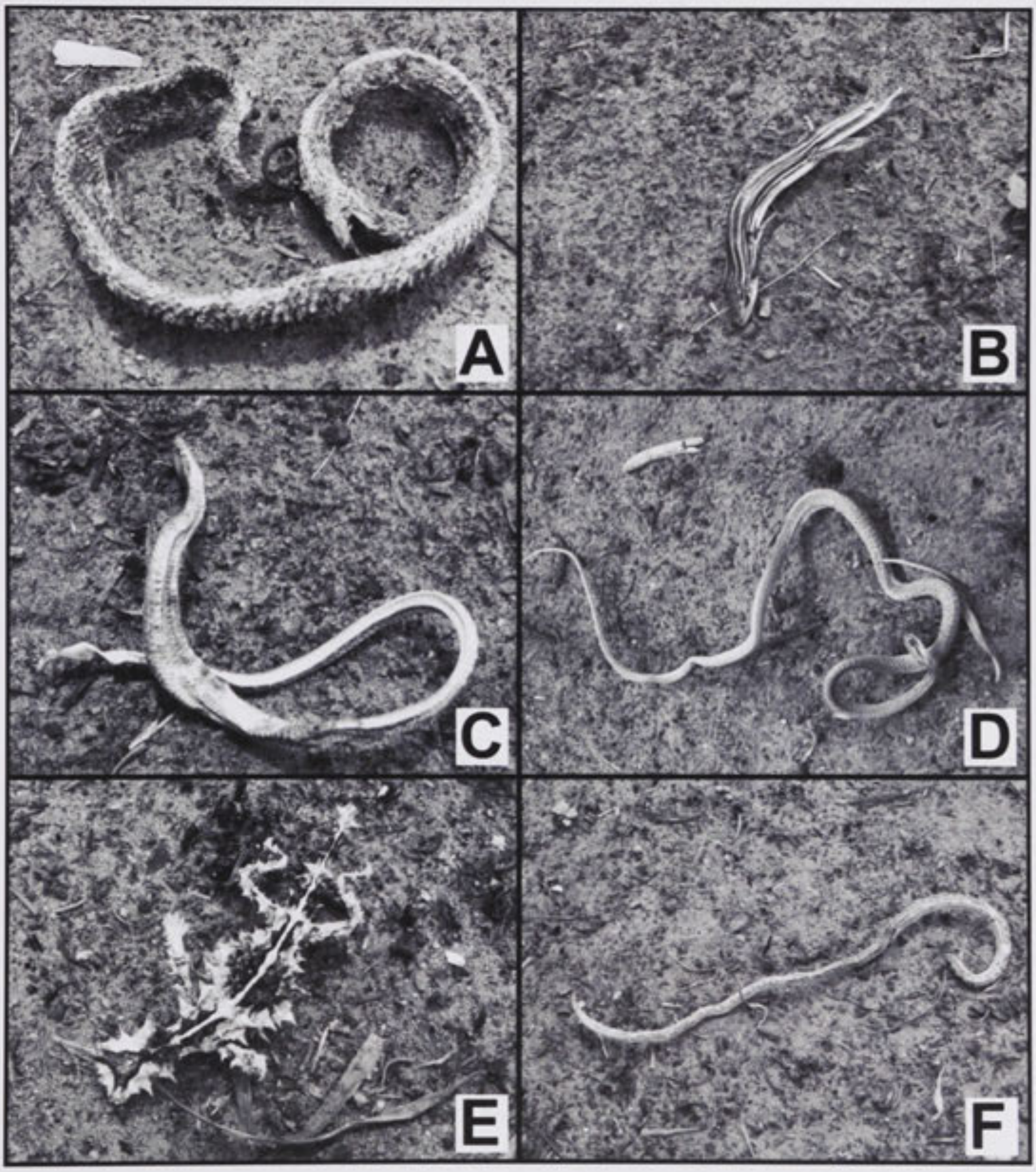
3.2 Main text

Effective fire management for biodiversity conservation requires an ability to predict how populations will respond to varying fire regimes (Whelan et al. 2002; Bradstock et al. 2006). Considerable research has documented animal responses to fire but the mechanisms behind the observed patterns are poorly understood making generalisations difficult (Driscoll et al. 2010). A key gap in our knowledge is the fate of animals during fire: do they survive by fleeing or sheltering underground, or are they killed by fire? Do certain ecological traits make some species more susceptible than others to mortality during fire? Answering these questions is critical to understand how fire management will affect different species. Published accounts of fire-induced mortality of vertebrates are rare in many parts of the world (Woolley et al. 2008), particularly Australia (Whelan et al. 2002). Some studies assume that rates of direct mortality are low (e.g. Rochester et al. 2010) while others assume higher mortality from absences of tagged individuals after fire (e.g. Driscoll & Roberts 1997). In Australian reptiles, the season of burning (Griffiths & Christian 1996; Kuchling 2007) and burrow use (Fenner & Bull 2007) may influence mortality rates during fire. Observations from a wider range of species will help determine if there are ecological traits that could influence mortality during fire. Here, we report results from a brief survey undertaken less than five weeks after a widespread, severe summer wildfire in which mortality of reptiles was recorded.

The survey took place in Pinkawillinie Conservation Park, South Australia (32° 54' 25" S, 135° 51' 08" E), a 130,148 hectare reserve with a semi-arid climate, dominated by mallee woodlands (multi-stemmed *Eucalyptus* species with a shrubby understorey). As part of a broader study of reptile fire ecology, six pitfall trapping stations had been established throughout the reserve. On 27th December 2005 a lightning-caused wildfire burned 28,154 hectares of the reserve, including four of our trapping stations. Maximum temperature on the day of the fire was 44ºC, with 15 % relative humidity and 57 km/hr winds (Bureau of Meteorology/J. Tilley, South Australian Department of Environment and Natural Resources). The fire began WSW of our trapping stations, initially covering 37 km in 9 hr under a WNW wind. Our survey site burnt under subsequent SW then SE winds at approximately 1-2 km/hr forward rate of spread, and although fire intensity was not quantified it was likely high (J. Tilley, pers. comm.). On 28th January 2006, 32 days after the fire, we surveyed an area adjacent to one of the trapping stations. The area, previously unburnt since 1986, was completely incinerated by the December 2005 fire and was approximately 500 m from the northern fire edge. Ten people, spaced 1-2 m apart, walked from an access track (also within the burned area) approximately 400 m towards the trapping station then back to the track along the same path, over a total survey time of 10-15 min.

During the survey, we recorded six dead individual reptiles from six species (Fig. 3.1): *Acanthophis antarcticus* (common death adder, Elapidae), *Ctenotus atlas* (Scincidae), *Delma petersoni* (Pygopodidae), *Demansia reticulata cupreiceps* (yellow-faced whipsnake, Elapidae), *Moloch horridus* (thorny devil, Agamidae), and *Pygopus lepidopodus* (common scaly-foot, Pygopodidae). *Acanthophis antarcticus* was blackened and scorched indicating direct mortality from fire. The other specimens were dried and shrivelled and may have been killed by fire, or died shortly afterwards. *Ctenotus atlas* and *P. lepidopodus* also had signs of predation. Two of the dead species were recorded in traps at the trapping station near our survey site prior to the fire (*C. atlas* and *M. horridus*). The remaining species (all snakes or legless lizards) were never recorded at that trapping station despite 1400 trap nights. We do not know the number of animals that survived the fire so our results cannot be translated into mortality rates, but they do suggest a wide range of species are killed by fire. Our survey was brief and covered a small area so the number of dead reptiles found could be considered high. Prior to the fire, dead reptiles were rarely (< 1 per week) encountered during daily walks to the trapping stations, even in other areas that had been recently burnt in prescribed fires or wildfires.

Fig. 3.1 Six reptile species were found dead during a brief survey of mallee four weeks after a wildfire: (A) *Acanthophis antarcticus*, (B) *Ctenotus atlas*, (C) *Delma petersoni*, (D) *Demansia reticulata cupreiceps*, (E) *Moloch horridus*, and (F) *Pygopus lepidopodus* (photos: B. Meulders).



There was one common trait among the species we recorded: they were all non-burrowing species that shelter in low vegetation and leaf litter (Wilson & Swan 2010), although some may occasionally use burrows of other species. Other reptiles commonly recorded from the trapping station near our survey site, but not found dead after the fire, included several burrowing species (*Brachyurophis semifasciatus*, *Liopholis inornata*, *Lucasium damaeum*, *Nephrurus stellatus*, *Ramphotyphlops bituberculatus*). Our observations support the suggestion that burrowing species have lower mortality than non-burrowers during wildfire. In a previous report, no mortality was recorded in one species of burrow-dwelling skinks during a fire (Fenner & Bull 2007). However, in another study, tortoises in burrows experienced 50 % mortality during wildfire (Kuchling 2007) so burrowing does not always offer protection from fire. We do not know the time of day that the fire burnt our survey area, but the dead animals recorded included nocturnal (*A. antarcticus*, *D. petersoni*, and *P. lepidopodus*) and diurnal species (*C. atlas*, *D. reticulata cupreiceps*, and *M. horridus*). Daily activity patterns may therefore not be useful predictors of reptile mortality during fire, but more data are needed to confirm this.

In monsoonal Australia, Griffiths and Christian (1996) found that early dry-season fires did not directly kill frillneck lizards, but late dry-season fires (which have higher intensity and severity) caused 29 % mortality. The fire that burnt our survey site was severe (all above ground vegetation was scorched). Some of the species we found dead are very slow moving (*A. antarcticus* and *M. horridus*) thus unlikely to escape fire by fleeing. However, *D. reticulata cupreiceps*, a swift predator, was similarly unable to escape the fire. High movement ability may have little benefit during intense, summer wildfires.

In summary, we found that six species of Australian reptiles suffered mortality during, or shortly after wildfire. Traits based on shelter sites may be better predictors of mortality during fire than daily activity patterns or movement ability, but further research is needed to confirm this. To enhance our understanding of fire-induced mortality, researchers should conduct controlled experiments during prescribed burning and take advantage of survey opportunities following wildfire (Lindenmayer et al. 2010). Studies of a wide range of species will allow relationships between ecological traits and mortality to be more rigorously tested, ultimately assisting the development of a predictive framework for fire management.

3.3 Acknowledgements

Thanks to Adam Aitken, Zonnetje Auburn, Phil Barron, Catherine Brown, Mel Cundy, Toby Galligan, Kylie Johnson, Christopher Lawson, Angela McGuire, and Alice Quarmby for their involvement in the survey. Mark Hutchinson at the South Australian Museum helped with reptile identification and Joe Tilley from the Pt Lincoln branch of the South Australian Department of Environment and Natural Resources (DENR) provided logistical support in the field. This research was supported by funds from the Australian Research Council, DENR, Flinders University, and the Australia and Pacific Science Foundation, and was conducted under research permit Q24788 (DENR).

3.4 References

Bradstock R.A., Bedward M. and Cohn J.S. (2006). The modelled effects of differing fire management strategies on the conifer *Callitris verrucosa* within semi-arid mallee vegetation in Australia. *Journal of Applied Ecology* 43: 281-292.

Driscoll D.A., Lindenmayer D.B., Bennett A.F., Bode M., Bradstock R.A., Cary G.J., Clarke M.F., Dexter N., Fensham R., Friend G., Gill A.M., James S., Kay G., Keith D.A., MacGregor C., Russell-Smith J., Salt D., Watson J.E.M., Williams R.J. and York A. (2010). Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation* 143: 1928-1939.

Driscoll D.A. and Roberts J.D. (1997). Impact of fuel-reduction burning on the frog *Geocrinia lutea* in southwest Western Australia. *Australian Journal of Ecology* 22: 334-339.

Fenner A.L. and Bull C.M. (2007). Short-term impact of grassland fire on the endangered pygmy bluetongue lizard. *Journal of Zoology* 272: 444-450.

Griffiths A.D. and Christian K.A. (1996). The effects of fire on the frillneck lizard (*Chlamydosaurus kingii*) in northern Australia. *Australian Journal of Ecology* 21: 386-398.

Kuchling G. (2007). Impact of fuel reduction burns and wildfires on the critically endangered western swamp tortoise *Peudemydura umbrina. Ecological Society of Australia Conference Proceedings,* Perth, Western Australia.

Lindenmayer D.B., Likens G.E. and Franklin J.F. (2010). Rapid responses to facilitate ecological discoveries from major disturbances. *Frontiers in Ecology and the Environment* 8: 527-532.

Rochester C.J., Berehme C.S., Clark D.R., Stokes D.C., Hathaway S.A. and Fisher R.N. (2010). Reptile and amphibian responses to large-scale wildfires in southern California. *Journal of Herpetology* 44: 333-351.

Whelan R.J., Rodgerson L., Dickman C.R. and Sutherland E.F. (2002). Critical life cycles of plants and animals: developing a process-based understanding of population changes in fire-prone landscapes. In: *Flammable Australia: the fire regimes and biodiversity of a continent.* (eds. Bradstock RA, Williams JE, Gill AM). Cambridge University Press, Cambridge.

Wilson S. and Swan G. (2010). *A Complete Guide to Reptiles of Australia*, 3 edn. New Holland, Sydney.

Woolley L., Millspaugh J.J., Woods R.J., Janse van Rensburg S., Mackey R.L., Page B. and Slotow R. (2008). Population and individual elephant response to a catastrophic fire in Pilanesberg National Park. *PLoS ONE* 3: e3233.

Chapter 4

Post-fire succession affects abundance and survival but not detectability in a knob-tailed gecko

Research Paper

Co-authors:
C. Michael Bull
Don A. Driscoll

I marked geckos with a fluorescent elastomer implant to identify individuals during recapture surveys. The position of the marks on the body identifies this gecko as NS-H3-195 (Photo A.L. Smith).

This chapter has been published:
Smith A.L., Bull C.M. and Driscoll D.A. (2012). Post-fire succession affects abundance and survival but not detectability in a knob-tailed gecko. *Biological Conservation* 145: 139-147.

4.1 Abstract

Altered fire regimes threaten the persistence of many animal species globally, thus understanding how fire affects demographic processes is critical for conservation. Using two years of mark-recapture data from the Australian gecko *Nephrurus stellatus*, we investigated the effect of fire on (i) detectability to reliably measure post-fire changes in abundance, and (ii) survival and reproductive rates to investigate the mechanisms of successional change. Data were collected from two conservation reserves each with three different fire categories based on time since the last fire. "Early", "medium" and "late" sites had 2-3, 7-9 and 42-48 years since fire, respectively. A robust design modelling framework was used to estimate the effect of fire category on abundance, survival and capture probability while also examining the influence of temperature and behaviour on detectability. Geckos showed trap-shy behaviour and detectability increased significantly with increasing temperature but was not affected by time since fire. Accounting for detectability, geckos were more abundant in the medium than the early sites, and were rare in the late sites. Although trends in survival are more difficult to address with short-term data, our results showed lower monthly survival rates, but higher fecundity in the early than the medium sites. These results were possibly related to successional changes in predation, the thermal environment, and food availability. We demonstrated how mark-recapture analysis can show the causes of animal fire responses while realistically accounting for detectability. Such information is necessary to provide a predictive framework to guide fire management for biodiversity.

4.2 Introduction

Disruption of natural fire regimes from modern human land use has contributed to the decline of animal populations in many ecosystems around the world (Pardon et al. 2003; Lyet et al. 2009; Betts et al. 2010; Gregory et al. 2010; Sanz-Aguilar et al. 2011). Fire is widely used to create successional diversity in vegetation under the often untested assumption that this will benefit biodiversity more broadly (Parr & Andersen 2006). However, if this practice is conducted at inappropriate spatial and temporal scales, animal populations may face local extinction (Templeton et al. 2001; Bradstock et al. 2005).

Well studied changes in plant demography after fire have led to conceptual and simulation based models to predict the effects of different fire regimes on vegetation (e.g. Bradstock et al. 2006; Moreira et al. 2009). Although there has been some progress in this direction for animal species (e.g. Bradstock et al. 2005) development has been slower than for plants because of the difficulty in obtaining animal life history data (Clarke 2008). At the community level, a functional trait-based approach for predicting fire responses in plants (e.g. Keith et al. 2007) holds promise for use in animal studies (Moretti et al. 2009; Langlands et al. 2011). However, this approach requires detailed information on life history traits, including survival, reproduction and dispersal (Langlands et al. 2011) which are not available for most animal species in fire-prone ecosystems. Understanding demographic changes of animal populations after fire is critical if we are to develop a predictive framework for ecological fire management (Clarke 2008).

Post-fire succession in animal communities has traditionally been explained by a habitat accommodation model where the peak density of an animal species is correlated with that of its optimal post-fire habitat (Fox 1982). However, fire-related patterns of abundance often vary spatially or temporally within species making simple habitat models unreliable (Driscoll & Henderson 2008; Lindenmayer et al. 2008). Understanding the causes of fire-related changes in abundance will allow more accurate predictions of the effects of fire regimes on animal populations (Whelan et al. 2002; Driscoll et al. 2010). The profound habitat changes caused by fire are likely to influence survival in animal species by changing predation rates, food availability, reproductive success and thermal environments (Le Galliard et al. 2005; Hossack et al. 2009; Hawlena et al. 2010). Recent evidence shows that modified fire regimes can affect animal survival (O'Brien et al. 2003; Pardon et al. 2003; Lyet et al. 2009) highlighting the need for a taxonomically and ecologically broader understanding of successional changes in survival rates of animals.

While developing a trait-based approach to fire management is crucial, quantifying the effects of fire on animal abundance remains fundamental to fire ecology. Ecological fire management plans are usually based on empirical observations of apparent differences in abundance of target species in habitats of different time since fire (e.g. Petty et al. 2007; DENR 2009). However, animals can also show behavioural responses to fire-driven succession (Vernes & Haydon 2001; Fenner & Bull 2007), meaning that detectability could change with time since fire. If this is true, descriptions of animal fire responses based solely on counts may not represent actual abundance, leading to misguided management (White 2005). Despite this concern very few studies have controlled for detectability when investigating the effects of fire on animal abundance (Driscoll et al. 2010).

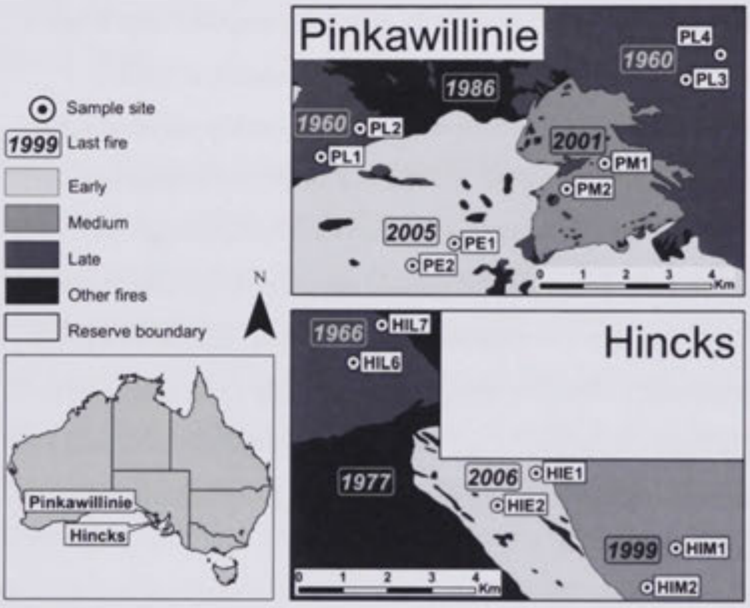
Driscoll and Henderson (2008) estimated abundance from counts to identify common reptile species with local distribution patterns influenced by post-fire succession in mallee woodlands of southern Australia. One of these was the starred knob-tailed gecko, *Nephrurus stellatus*, which they reported to show a strong fire-specialist response, with higher abundance in early than late successional habitats (Driscoll & Henderson 2008). In this study we collected two years of mark-recapture data from *N. stellatus* to determine if (1) apparent effects of succession on abundance were confounded with fire related detectability differences, and (2) monthly survival rates differed with time since fire and could therefore account for observed differences in abundance. We also examined if post-fire succession affected three measures of reproductive capacity (age structure, sex ratio and female reproductive status) to help further explain any observed fire effects on abundance and survival. Our aim was to understand demographic responses to fire in a species that is likely to be sensitive to variation in fire regimes. Through this process, we sought to advance fire research on animals by developing a causative understanding of succession using biologically meaningful models of detectability.

4.3 Methods

4.3.1 Study system

The study was conducted at Hincks Wilderness Area and Pinkawillinie Conservation Park on the Eyre Peninsula, South Australia (Fig. 4.1). The region is semi-arid, with an average annual rainfall of 322 mm. The main topographic features are white siliceous sand dunes, occurring in either large, parabolic fields or longitudinal ridges over calcrete limestone (Twidale & Campbell 1985). Hincks and Pinkawillinie are dominated by mallee woodlands where low, multi-stemmed *Eucalyptus* species (predominantly *E. incrassata*, *E. brachycalyx* and *E. socialis*) are associated with the shrubs *Melaleuca* *uncinata*, *Callitris verrucosa* and the spiky hummock grass *Triodia irritans* (Specht 1972; Robinson & Heard 1985). Summer lightning, the most common ignition source of mallee, typically results in large, severe wildfires on a decadal time scale (Bradstock & Cohn 2002). Records of the complex fire histories of the two reserves have been kept by the South Australian Department for Environment and Natural Resources for over 40 years (DENR 2011).

Fig. 4.1 Location of the sites where *Nephrurus stellatus* were sampled at Hincks Wilderness Area and Pinkawillinie Conservation Park on the Eyre Peninsula, South Australia.



Nephrurus stellatus is distributed widely across the Eyre Peninsula and in a small area of central-south Western Australia (Wilson & Swan 2008). It is common in sandy areas, residing in self-dug burrows by day and actively foraging for invertebrate prey by night (Cogger 1996). Driscoll and Henderson (2008) captured *N. stellatus* consistently more often in recently burnt (3-7 yr since the most recent fire) than long unburnt (18-39 yr since the most recent fire) habitat across five conservation reserves. Little is known of the life history, but preliminary skeletochronological analysis suggests individuals can live for up to four years in the wild, possibly longer (A.L. Smith, unpublished data).

4.3.2 Trapping protocol

At each reserve we established two sample sites in each of three fire categories based on time since last fire. "Early" sites had 2-3 yr since fire at the time of first data collection (2008), "medium" sites had 7-9 yr and "late" sites had 42-48 yr (Fig. 4.1). Sites were selected to ensure that other factors were similar, particularly the presence of sandy soil and *T. irritans*, an important habitat plant for many reptiles. In anticipation of low capture rates at the late sites (Driscoll & Henderson 2008), two additional late sites were sampled at Pinkawillinie (Fig. 4.1). At each site 25 pitfall traps were set in a 1 ha plot, with five rows of five traps spaced at 25 m intervals. The distance between traps was based on typical movement distances (mean 16, range 0-103 m/day) from preliminary radio-tracking and mark-recapture studies. Traps consisted of 20 l buckets buried flush with the ground and intersected by a 10 m long, 30 cm high plastic drift fence. Fences alternated in angle so that each fence was perpendicular to the adjacent fences. Trapped animals could shelter in a 15 cm long half PVC pipe placed at the bottom of each bucket, covered with a 15 x 25 cm wood block which also acted as a floating refuge in case of heavy rain. Two temperature loggers (Gemini) in the shade at each reserve recorded temperature every hour during the trapping sessions. Readings from the two loggers were averaged.

We defined a field season as the spring-summer period when the geckos were most active and conducted our study over two seasons (Nov 2008 – Feb 2009 and Nov 2009 – Feb 2010). We collected capture data under Pollock's (1982) robust design where, in each field season, a series of three primary capture sessions incorporated several trap days, or secondary capture occasions (Kendall et al. 1995). Primary sessions included 5 to 15 secondary occasions (mean = 8). During each primary session traps in all fire categories were opened and closed at the same times. The intervals between primary sessions ranged from 0.5 to 1.9 months within seasons and from 8.8 to 9.6 months between seasons. Under this design abundance and detectability could be estimated from within primary sessions when the population was assumed to be closed to gains and losses (Kendall et al. 1995). Survival could be estimated from the intervals between the sessions when the population was assumed to be open (Kendall et al. 1995). This design allowed us to estimate survival rates during the activity season of the geckos, and between seasons when the geckos were mostly inactive. We treated data from each reserve separately as they were sampled at different times within seasons when daily temperatures varied and because capture rates in reptiles are strongly dependent on temperature. Traps were checked every morning between 0600 and 1000 hr and all captured geckos (Supporting material 4.9.1) were taken to a base for processing where they were held for up to 24 hr. Animals were therefore unavailable for capture on the secondary occasion following their capture. This may have biased rates of capture probability, but the effect was considered minor compared to the total length of the study and was consistent across fire categories. Only low rates of temporary emigration were evident during the trapping sessions (see 4.4 Results), so the bias caused on this parameter should also be minimal.

Size (snout-vent length) to sexual maturity (male = 55 mm, female = 70 mm) was established by examining reproductive organs in 81 *N. stellatus* specimens at the South Australian Museum, following Godfrey and Hutchinson (2010). Geckos captured in the field were then measured and scored as either adult or juvenile. Adult sex was determined by external hemipenal bulges, present in males but not females. Adult females were scored as gravid when well developed eggs were visible.

For each initial capture, a single toe tip from the back foot was clipped as a batch mark, unique to each season (Funk et al. 2005). We used a Visible Implant Elastomer kit (Northwest Marine Technology) to apply a unique visual mark to each gecko by injecting a small amount of fluorescent elastomer under the ventral skin surface. Using different ventral positions allowed us to individually mark up to 300 animals annually. We rarely (3% of recaptures) found an animal with a clipped toe and an unreadable mark, indicating a high rate of mark retention. When a mark was not readable (in nine between-season recaptures when the animal had grown substantially) we sampled additional tissue and used microsatellite DNA genotypes (Smith et al. 2011) to match it to a capture from the previous year. These animals were re-marked with a new number. Each animal was released 5 – 10 m from the trap where it had been captured. If released during daylight, the gecko was placed in a concealed burrow and monitored to ensure it continued to dig itself in. Individuals that died in traps (1.3 % of sampled animals) were not included in the analysis.

4.3.3 Habitat data

To quantify habitat differences among fire categories, we surveyed sites for structural vegetation characteristics and dominant species. At each site we established 25 10 m^2 (2 x 5 m) plots on the NE side of each pitfall trap with a 2 m buffer between the plot and the trap fence. We recorded percentage canopy cover of trees (> 2 m), tall shrubs (0.5-2 m), low shrubs (< 0.5 m), dead (burnt) trees (> 2 m), bare ground and leaf litter. We also recorded the percentage cover of the dominant plant species: *Eucalyptus sp*., *M. uncinata*, *C. verrucosa* and *T. irritans*. We analysed vegetation variables with Principal Components Analysis in the base package of R 2.12 (R Development Core Team 2010) to illustrate similarities and differences among sites.

4.3.4 Reproductive capacity

Using initial capture data from each season and location separately, we applied Fisher's exact tests to determine if fire category influenced the age structure (ratio of juveniles to adults), sex ratio, and the reproductive status of adult females (detailed methodology in Supporting material 4.9.2).

4.3.5 Mark-recapture analysis

To estimate abundance, survival and detectability, we used the full-likelihood robust design model which includes the parameters capture probability (p), recapture probability (c), temporary emigration (γ), abundance (N) and survival (S) (Kendall et al. 1997). Temporary emigration has two components: γ'', the probability of being unavailable at time *i* for animals that are on the study area at time *i*-1, and γ', the probability of being unavailable at time *i* for animals that are off the study area at time *i*-1 (Kendall et al. 1997). It is therefore possible to model random ($\gamma''=\gamma'$) and Markovian ($\gamma''\neq\gamma'$) temporary emigration under the robust design (Kendall et al. 1997).

Complex group structures in our data (i.e. sex, age, and site in addition to fire category groups) led to over parameterised models, giving us little power to detect fire effects on the parameters. To keep *n*/*K* ratios high (where *n* is the number of captures and *K* the number of parameters) we pooled data from the paired sites within each fire category, and from the four sites in the late category at Pinkawillinie. Parameter estimates were thus based on four hectares for the late category at Pinkawillinie and two hectares for all other units. Data from age and sex categories were also pooled. This was justified by preliminary analyses from both reserves, which showed low support for sex and age differences in capture probability.

For each primary session separately, we tested the assumption that the populations were closed using CLOSETEST 3 (Stanley & Richards 2005). We tested the goodness-of-fit of a global model using RDSURVIV (Hines 1996; Kendall & Hines 1999). It is not possible to include group structure in this model, so we used the pre-defined model which accounted for time effects on survival, time and behaviour effects on capture probability (either trap-happiness or trap-shyness) and for constant, random temporary emigration. The variance inflation factor $\hat{c}$ was calculated for the global model as χ^2/df, which was used to adjust for overdispersion in our data.

We used the R package RMark 2.0 (Laake & Rexstad 2008) to build models with script for fitting, selection and parameter estimation in program MARK 5.1 (White & Burnham 1999). We took an information theoretic approach and used $\mathrm{QAIC_c}$ (which accounts for overdispersion and is recommended for small samples) to select the most parsimonious model in our candidate set (Burnham & Anderson 2002). To assess the relative likelihood of each model in the candidate set we calculated Akaike weights (w_i) (Burnham & Anderson 2002).

We developed a set of a priori hypotheses to investigate the effects of fire category on the parameters while also accounting for possible effects of temperature, trap-related behaviour and temporal variation (Burnham & Anderson 2002). The effect of temperature on capture probability was modelled using daily minimum temperature (mt) for each secondary occasion (Table 4.1). Variation in capture probability over primary sessions was modelled by numbering the sessions from one to six (sn) (Table 4.1). We envisaged that the capture process could affect recapture rates by leading to either a trap-happy ($p<c$) or trap-shy ($p>c$) behavioural response. We thus examined capture probability models with ($p\neq c$) and without ($p=c$) trap related behaviour effects (Otis et al. 1978). We tested whether animals moved off the study area making a proportion of the population temporarily unavailable for capture during each primary session. Two time-constant models of temporary emigration were explored: no temporary emigration ($\gamma''=\gamma'(0)$), and random temporary emigration ($\gamma''=\gamma'(.)$) (Table

4.1) (Kendall et al. 1997). Time-varying and Markovian models of temporary emigration were not included in the candidate set as their *n*/*K* ratio was too low. To investigate meaningful effects of time on survival while keeping *n*/*K* high, we allocated one of two parameters to each interval between primary sessions (sw) (Table 4.1). The "summer" parameter described monthly survival rates in the short intervals (mean = one month) within seasons when geckos were active. The "winter" parameter described monthly survival rates in the longer time intervals (mean = 9.2 months) between seasons when geckos were mostly inactive. Temporal changes in abundance over primary sessions (sn) were investigated and fire category group effects (g) were modelled for p, c, N, and S (Table 4.1). Our global model was p(mt+sn+g), c(mt+sn+g), $\gamma''=\gamma'(.)$, S(sw+g), N(sn+g+sn*g).

Table 4.1 Variables used to parameterise capture (p) and recapture (c) probability, temporary emigration (γ), abundance (N) and survival (S).

Variable	Notation	Values	Used to parameterise
Minimum temperature	mt	Degrees Celsius	p, c
Primary session	sn	1-6 for each primary session	p, c, N
Fire category group	g	Early, medium, late	p, c, N, S
Season	sw	Summer or winter (monthly rates)	S
Constant	.	No variation	p, c, γ, N, S

The candidate set for each parameter included its global formulation and all models nested within it, including constant, or "dot" models (.). Using the step-down modelling approach of Lebreton et al. (1992) (discussed in Doherty et al. 2011), we determined the top model for each parameter sequentially. To begin, candidate models for capture probability were fitted while keeping the global parameterisation of γ, N and S constant (Supporting material 4.9.3). We then fitted candidate models for γ, S and N, in that order, with the other parameters updated based on information from model selection in previous steps. The final model with the lowest $QAIC_c$ was used for parameter estimation. Our analysis allowed us to determine the importance of fire on abundance and survival in *N. stellatus* using realistic models for capture probability and temporary emigration.

4.4 Results

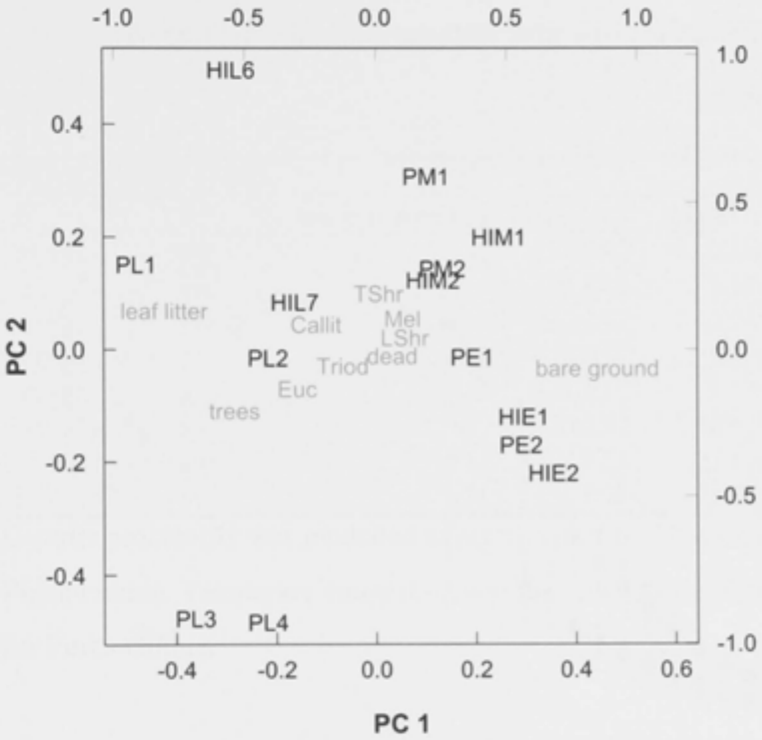
4.4.1 Capture summary, reproductive capacity, and robust design assumptions

We recorded 532 captures (308 individuals, 224 recaptures) at Hincks and 215 captures (139 individuals, 76 recaptures) at Pinkawillinie (Supporting material 4.9.1). There was no effect of fire category on the age structure or sex ratio in either season or location (Fisher's exact tests $P > 0.05$, Supporting material 4.9.2). The proportion of females that were gravid was significantly higher in the early (93.8%) than the medium fire category (56.5%) in season two at Hincks (Fisher's exact test $P = 0.01$, Supporting material 4.9.2). Data from Pinkawillinie and from both sites in season one were too sparse for reliable inferences (Supporting material 4.9.2). All primary trapping periods in both data sets met the assumptions of closure (CLOSETEST: $P > 0.05$). Goodness-of-fit tests indicated that a general model fitted the data for Hincks ($\chi^2 = 14.28$, df = 11, $P = 0.22$) and Pinkawillinie ($\chi^2 = 11.42$, df = 6, $P = 0.08$), with some evidence of overdispersion. We therefore adjusted $\mathrm{QAIC_c}$ values and standard errors for Hincks ($\hat{c} = 1.3$) and for Pinkawillinie ($\hat{c} = 1.9$).

4.4.2 Habitat variation

The first two components (PC) of the Principle Components Analysis explained a cumulative total of 90% of the variation in the vegetation plot data (PC1 = 83%, PC2 = 7%, Fig. 4.2). There was a clear separation between the late sites and the other sites along PC1. Ground cover variables appeared to contribute most to this separation, with leaf litter replacing bare ground with increasing time since fire (Fig. 4.2). The early and medium sites were separated mainly along PC2. There was more variation in vegetation among the late sites as they covered the full extent of PC2, while the early and medium sites were more centrally clustered (Fig. 4.2). There was little separation between reserves within fire categories indicating similar vegetation structure at both locations (Fig. 4.2).

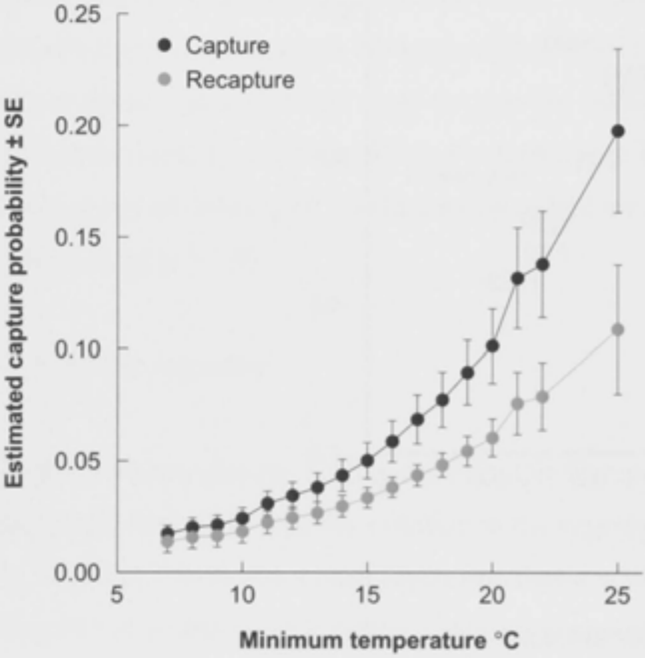
Fig. 4.2 Principle Components Analysis of vegetation structure and dominant plant species for each study site. Principle component 1 (PC1) explained 83% of the variation in the data, and PC2 explained 7%. The names of the study sites are shown in black, and the measured variables in grey (TShr = tall shrubs, LShr = low shrubs, Mel = *Melaleuca uncinata*, Callit = *Callitris verrucosa*, dead = dead trees, Triod = *Triodia irritans*, Euc = *Eucalyptus spp*.).



4.4.3 Model selection and parameter estimates

Of the 14 models for capture probability at Hincks, the most parsimonious was p(mt), c(mt) ($w_i = 0.399$) (Supporting material 4.9.3). Capture probability increased significantly with increasing minimum temperature and geckos which had previously been captured had a lower capture probability than geckos on their first capture, indicating a trap-shy behavioural response (Fig. 4.3). Our n/K ratio for Pinkawillinie was very small (7 for the global model) and several of our models for capture probability were too general for our data. The two models with the lowest $QAIC_c$ included trap-related behaviour effects but these both failed to produce estimates and standard errors for N. We thus chose the best fitting model with parameter estimates for N (p(mt), $w_i = 0.085$, Supporting material 4.9.3) as our top model for capture probability at Pinkawillinie. There was little support for an effect of fire category on capture probability at either Hincks or Pinkawillinie (Supporting material 4.9.3). Of the two models for temporary emigration (constant and zero) there was support for temporary emigration at Hincks ($w_i = 0.664$) with the proportion of animals unavailable for capture in each primary period estimated at 0.093 (± 0.090 SE). The model for no temporary emigration had the most support for Pinkawillinie ($w_i = 0.761$).

Fig. 4.3 Estimated capture (p) and recapture (c) probability (± SE) increased with increasing minimum temperature in *Nephrurus stellatus* at Hincks and trap-shy behaviour (p>c) was detected.



No *N. stellatus* were captured in the late category at Hincks, restricting comparisons from that location to the early and medium categories. At both Hincks and Pinkawillinie abundance was best explained by fire category and primary session (Table 4.2). There were significant differences in abundance among primary sessions, even within seasons, at both locations (Fig. 4.4). Abundance was consistently lower in the early than the medium sites at Hincks (Fig. 4.4a). Despite twice the trapping effort, the late category at Pinkawillinie had consistently lower abundance (mean population density = 0.7/ha) than the early (7.8/ha) and medium (14.7/ha) categories (Fig. 4.4b).

Table 4.2 Candidate models for abundance (N) and survival (S) of *Nephrurus stellatus* at Hincks and Pinkawillinie.

HINCKS

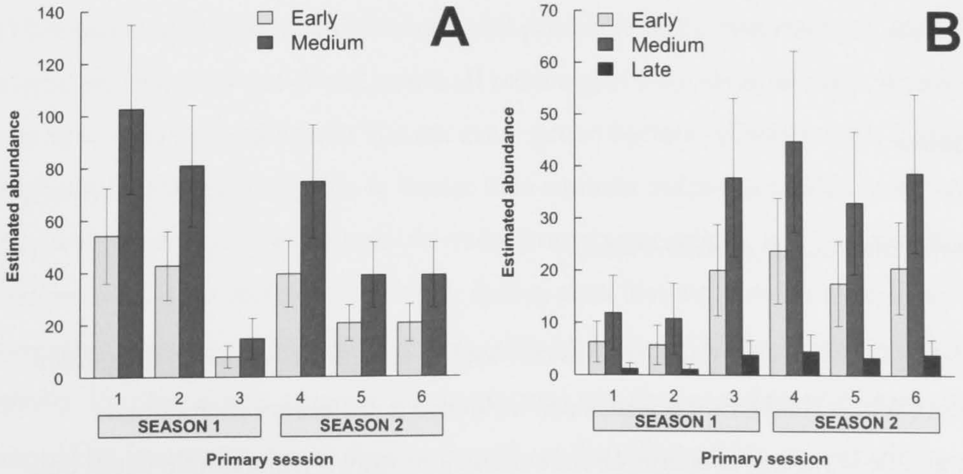
N	S	no. parameters	QAICc	Δ QAICc	weight	QDeviance
sn+g	sw+g	15	688.283	0.000	0.937	615.220
sn+g+sn*g	sw+g	20	693.998	5.715	0.054	610.221
sn+g	sw	14	698.229	9.946	0.006	627.283
sn	sw+g	14	700.305	12.022	0.002	629.359
g	sw+g	10	707.852	19.569	< 0.001	645.297
sn+g	g	14	715.861	27.578	< 0.001	644.916
.	sw+g	9	719.138	30.855	< 0.001	658.660
sn+g	.	13	720.778	32.495	< 0.001	651.942

PINKAWILLINIE

N	S	no. parameters	QAICc	Δ QAICc	weight	QDeviance
sn+g	sw	12	331.982	0.000	0.616	152.769
g	sw	7	333.883	1.901	0.238	165.674
sn+g	sw+g	14	335.297	3.315	0.117	151.529
sn+g	.	11	338.537	6.556	0.023	161.569
sn+g	g	13	341.637	9.655	0.005	160.158
sn+g+sn*g	sw	22	350.487	18.506	< 0.001	147.549
.	sw	5	353.651	21.669	< 0.001	189.696
sn	sw	10	355.003	23.021	< 0.001	180.256

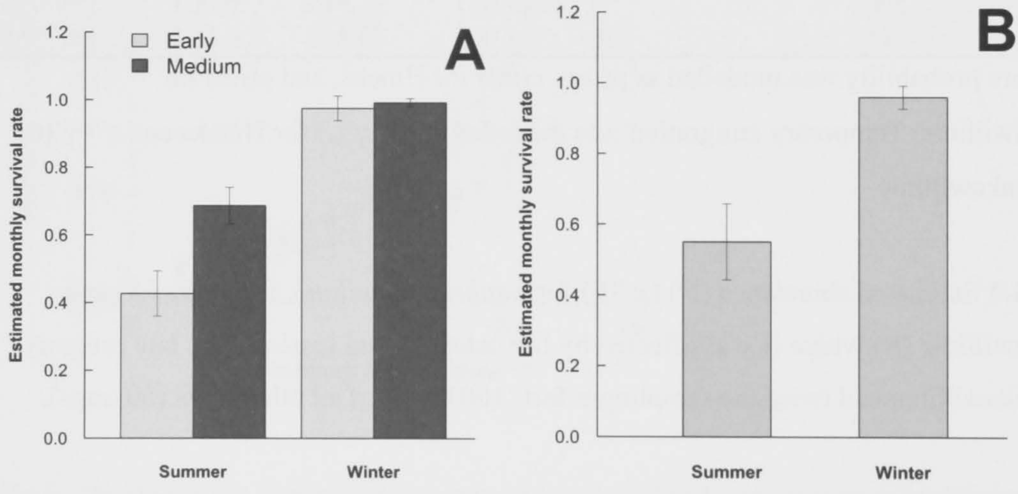
Capture probability was modelled as p(mt), c(mt) for Hincks, and p(mt) for Pinkawillinie. Temporary emigration was modelled as γ"=γ'(.) for Hincks and γ"=γ'(0) for Pinkawillinie.

Fig. 4.4 Estimated abundance (N) (± SE) for *Nephrurus stellatus* at Hincks (A) and Pinkawillinie (B) where N was affected by fire category and session. The late category at Pinkawillinie had twice the sampling effort (100 traps) of all other units (50 traps).



At both reserves there was strong support for seasonal differences in monthly survival rates (Table 4.2). Survival was significantly lower in summer than winter (Fig. 4.5a,b). At Hincks there was an additive effect of fire category (Table 4.2), with summer survival significantly lower in the early sites than the medium sites (Fig. 4.5a). There was no difference in survival between fire categories over winter (Fig. 4.5a). At Pinkawillinie, the best fitting model with fire effects on survival had only minimal support ($w_i = 0.117$), but showed lower mean summer survival rates in the late (0.309 ± 0.281 SE) than the early (0.477 ± 0.159 SE) and medium (0.601 ± 0.116 SE) sites. Although, these were not significant differences, the large variance resulting from data limitations may have masked an effect of fire category on survival.

Fig. 4.5 Estimated monthly survival rates (± SE) for *Nephrurus stellatus* at Hincks (A) and Pinkawillinie (B). At Hincks survival was affected by fire category and season, and at Pinkawillinie by season only.



4.5 Discussion

4.5.1 Post-fire abundance and detectability

Ignoring detectability in ecological studies can lead to spurious results and misguided management (White 2005). Fire regimes can influence detectability in mammals (Pardon et al. 2003) raising concerns about conclusions drawn from simple count data in fire ecology studies. We asked whether the early successional distribution of the gecko *N. stellatus* reported by Driscoll and Henderson (2008) was biased by differences in detectability among post-fire successional stages. Our mark-recapture analysis found no differences in detectability among fire categories. However, we observed a general trap-shy response in *N. stellatus*, probably because they learn to avoid stressful confinement in traps (Langkilde & Shine 2006).

The significant effects of time since fire on estimated abundance of *N. stellatus* were consistent across all six primary sessions at both reserves, supporting Driscoll and Henderson (2008) who reported higher capture rates of *N. stellatus* in recently burnt than long unburnt habitat. We added further resolution to the successional trajectory by including early, medium and late fire categories. Vegetation structure was clearly different among post-fire categories, but similar among sites in the same fire category in the two reserves. Abundance increased from the early to the medium category and was lowest in the late category, implying a mid-successional fire response in *N. stellatus*. However, mallee vegetation may remain unburnt for over a century (Haslem et al. 2011). In that context, *N. stellatus* could be regarded as an early successional species relative to the normal longevity of its habitat.

4.5.2 Mechanisms of abundance variation

Geckos in early sites had lower survival rates during the summer activity season than in medium sites, which probably contributed to the lower abundance in the early fire category. The early sites had only small shrubs, little leaf litter, and extensive bare ground, probably exposing geckos to higher predation. Changes in predation rates with habitat succession have been reported for mammals (Conner et al. 2011) and reptiles (Hawlena et al. 2010). Common nocturnal predators in the two reserves, including elapid snakes, owls and foxes, could all reduce gecko survival, as could diurnal predators like varanid lizards that excavate gecko burrows (Olsson et al. 2005). The higher monthly survival rates in winter than summer support a predation hypothesis. *Nephrurus stellatus* remain inactive underground over winter, with low predation risk but probably have increased mortality during peak activity periods in summer from predation, disease and extreme heat, as other reptiles do (Shine 1980; Bonnet et al. 1999). The fire effects on predator populations and the cascading impact on their prey should be incorporated into future research on the effect of fire on animal survival.

Although survival and abundance were lower in early sites, fecundity appeared to be elevated as indicated by the higher proportion of gravid females at Hincks. Both surface and burrow temperatures are most likely higher in recently burnt areas than in habitats with advanced succession (Hossack et al. 2009) which could increase fecundity (Chamaillé-Jammes et al. 2006) and hasten embryo development (Angilletta et al. 2000). Diurnal temperatures influence many reproductive parameters in nocturnal geckos including nest success (Pike et al. 2010) and offspring sex ratios (Gamble 2010). The higher proportion of gravid females in the early sites at Hincks could be a result of favourable thermal conditions. In addition, the early sites in this study had higher invertebrate abundance (Teasdale pers. comm.) and the reduced vegetation structure could increase foraging success (Vernes & Haydon 2001). Thus the early sites may have a thermal environment enhancing reproductive output in *N. stellatus*, plus a higher food resource base to increase fecundity. Although we found no effect of fire on sex ratios, the measures we used were limited by the difficulty in determining the sex of juveniles.

Although fecundity was higher, it did not result in increased abundance or a higher ratio of juveniles to adults in the early sites, suggesting high juvenile mortality that countered increased fecundity. Survival of lizard eggs can decrease if critical temperature and moisture thresholds are exceeded (Warner & Shine 2009). Thus, even though the early sites had a higher reproductive capacity, survival of the eggs, once laid, might be diminished in a thermally extreme habitat. Hatchlings would also be particularly vulnerable to desiccation and predation in the exposed habitat of the early sites.

There were temporal changes in abundance over the study period, but no interactive effects between fire category and primary session to indicate population growth rates varied among successional stages. Abundance (for no obvious reason) declined at Hincks over the two years but stayed stable at Pinkawillinie, at least over the final four sessions. Our two year study was too short to clarify how succession influences population growth rates in a perennial species like *N. stellatus* (Pianka 1970). A substantially larger data set is required for mark-recapture analyses which incorporate a recruitment parameter to model the effect of fire on population growth (Pradel 1996).

Mortality cannot be separated from permanent emigration using only mark-recapture data (Pollock et al. 1990), thus lower survival rates in the early sites could also reflect higher rates of dispersal. The influence of successional changes on patterns of dispersal needs more study. The effect of fire on survival that we observed is likely to be related to successional changes in predation, the thermal environment, and resource availability. Examining the relative contribution of these mechanisms will be necessary to advance our understanding of animal survival at different post-fire stages.

4.5.3 Declines in long-unburnt mallee

We found a substantial decline of *N. stellatus* in old mallee habitat. At Pinkawillinie, although there was minimal support for models with fire effects on survival, those models showed lower mean summer survival rates in the late sites. Small population numbers in those sites reduced precision in the estimates, but lowered survival rates could drive abundance declines in long unburnt sites. Reproductive success may decrease if advanced habitat succession limits opportunities for optimal nest site choice and thermoregulation (Pike et al. 2010). In addition, the dense leaf litter, and high *Triodia* and tree canopy cover may inhibit dispersal and movement, making it harder for individuals to forage and find mates. Quantifying the effect of fire on reproduction, dispersal and movement is essential to better understand the processes behind fire responses in species with specialist successional niches.

Our investigation of detectability in long unburnt mallee was limited at both study locations. At Hincks no geckos were captured in the late sites. At Pinkawillinie, models with fire effects on capture probability had little support, although estimates from the best fitting model with fire effects on capture probability (p(mt+g)) revealed higher values in the late than the early and medium categories but very large standard errors (Supporting material 4.9.3). The limited power of our data in the late category might have masked an effect of fire on detectability. Since we trapped late sites intensively at Pinkawillinie it is unlikely that continued trapping would greatly increase the precision of capture probability estimates. Focussing on direct measures of movement, through radio-tracking or direct observation, may provide a better idea of whether detectability differs between recently and long unburnt habitat (Koch & Hero 2007). Alternatively, an occupancy approach across a large number of sites may provide more information about detection differences among fire categories (MacKenzie et al. 2005).

4.6 Conclusions

Given the recent severe changes in land use, ecological fire management must be conducted on temporal and spatial scales that are appropriate to the contemporary landscape (Keith & Henderson 2002). In Australia, most mallee vegetation has been cleared for agriculture and small habitat remnants (approx. 1000 ha) can be completely incinerated by unplanned fire (DENR 2011), which may disadvantage late successional species (Driscoll & Henderson 2008). Prescribed burning may therefore be particularly important for small remnants which are at risk of complete incineration. Fire would best be used to protect late successional habitats on which many mallee animals rely (Friend 1993; Bradstock et al. 2005; Driscoll & Henderson 2008; Brown et al. 2009) and our data show that such management actions will also benefit early/mid-successional species. Where prescribed fire is not practical or appropriate, other actions such as canopy thinning may provide an alternative management strategy for providing fire breaks (Pike et al. 2011), although their effects on the broader community need to be assessed.

Understanding the effects of fire on animal population dynamics is fundamental to effective conservation planning in fire-prone ecosystems around the world (Clarke 2008). The development of accurate predictive models for fire management relies on our ability to understand not only patterns, but also processes behind fire responses in animal communities (Whelan et al. 2002; Driscoll et al. 2010). Our study questioned previous research on fire ecology in reptiles, which has typically reported fire related distributions based on simple count-based abundance estimates. By incorporating realistic models for detectability in our study of *N. stellatus*, our results showed that counts from pitfall trap data (e.g. Driscoll and Henderson 2008) can provide a reliable picture of post-fire abundance of reptiles. The early post-fire environment lowered survival rates in *N. stellatus* but high fecundity and increasing vegetation cover probably drove the populations towards a peak in both abundance and survival at approximately eight years after fire. A continued focus on the demographic effect of fire will increase our ability to effectively guide fire management for biodiversity conservation (Driscoll et al. 2010).

4.7 Acknowledgements

Assistance with field work was warmly received from J. Atamanik, S. Barnes, D. Barry, B. Berthelot, S. Blight, J. Bradley, A. Castañeda, S. Chubb, K. Coley, S. Dalgairns, A. De Costa, R. Dudaniec, L. Fazzalari, A. Fenner, K. Griffiths, I.J. Hagen, T. Hague, A. Hodgson, A. Johnston, S. Juárez, J. Lazzari, T. Ling, N. Maurovic, K. Mayes, K. McCallum, G. McLachlan, S. Morley, I. Motzke, T. Moyle, A. Murphy, K. Pelgrim, A. Quarmby, S. Scrivens, N. Shea, J. Simons, S. Smith, S. South, T. Suich, A. Talaba, L. Teasdale, M. Thomas, J. von zum Hof, H. Wahjudi, T. Wen, and C. Whitehead. Samantha Blight and Mark Hutchinson helped collect data on size to sexual maturity. Thanks to members of the Pt. Lincoln Department of Environment and Natural Resources, particularly Joe Tilley for logistical support in the field. We received valuable help with RMark from Jeff Laake via phidot.org/forum, and with RDSURVIV from Jim Hines. Three anonymous referees helped to improve the manuscript. This study was supported by funds from the Australian Research Council and conducted under scientific permit S25589 (Government of South Australia) and animal ethics permit E256 (Flinders University).

4.8 References

Angilletta M.J., Winters R.S. and Dunham A.E. (2000). Thermal effects on the energetics of lizard embryos: implications for hatchling phenotypes. *Ecology* 81: 2957-2968.

Betts M.G., Hagar J.C., Rivers J.W., Alexander J.D., McGarigal K. and McComb B.C. (2010). Thresholds in forest bird occurrence as a function of the amount of early-seral broadleaf forest at landscape scales. *Ecological Applications* 20: 2116-2130.

Bonnet X., Naulleau G. and Shine R. (1999). The dangers of leaving home: dispersal and mortality in snakes. *Biological Conservation* 89: 39-50.

Bradstock R.A., Bedward M. and Cohn J.S. (2006). The modelled effects of differing fire management strategies on the conifer *Callitris verrucosa* within semi-arid mallee vegetation in Australia. *Journal of Applied Ecology* 43: 281-292.

Bradstock R.A., Bedward M., Gill A.M. and Cohn J.S. (2005). Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. *Wildlife Research* 32: 409-423.

Bradstock R.A. and Cohn J.S. (2002). Fire regimes and biodiversity in semi-arid mallee ecosystems. In: *Flammable Australia: the fire regimes and biodiversity of a continent.* (eds. Bradstock RA, Williams JE, Gill AM). Cambridge University Press, Cambridge.

Brown S., Clarke M. and Clarke R. (2009). Fire is a key element in the landscape-scale habitat requirements and global population status of a threatened bird: the mallee emu-wren (*Stipiturus mallee*). *Biological Conservation* 142: 432-445.

Burnham K.P. and Anderson D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer-Verlag, New York.

Chamaillé-Jammes S., Massot M., Aragón P. and Clobert J. (2006). Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. *Global Change Biology* 12: 392-402.

Clarke M.F. (2008). Catering for the needs of fauna in fire management: science or just wishful thinking? *Wildlife Research* 35: 385-394.

Cogger H.G. (1996). *Reptiles and amphibians of Australia.* Reed, Port Melbourne, VIC.

Conner L.M., Castleberry S.B. and Derrick A.M. (2011). Effects of mesopredators and prescribed fire on hispid cotton rat survival and cause-specific mortality. *Journal of Wildlife Management* 75: 938-944.

DENR (2009). *Fire Management Plan: Reserves of the Southern Eyre Peninsula.* Department of Environment and Natural Resources. http://www.environment.sa.gov.au/firemanagement/Fire_management/Fire_planning/Adopted_fire_mgt_plans (accessed September 2011).

DENR (2011). *NatureMaps* Department of Environment and Natural Resources. http://www.naturemaps.sa.gov.au/ (accessed September 2011).

Doherty P.F., White G.C. and Burnham K.P. (2011). Comparison of model building and selection strategies. *Journal of Ornithology.*

Driscoll D.A. and Henderson M.K. (2008). How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model. *Biological Conservation* 141: 460-471.

Driscoll D.A., Lindenmayer D.B., Bennett A.F., Bode M., Bradstock R.A., Cary G.J., Clarke M.F., Dexter N., Fensham R., Friend G., Gill A.M., James S., Kay G., Keith D.A., MacGregor C., Russell-Smith J., Salt D., Watson J.E.M., Williams R.J. and York A. (2010). Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation* 143: 1928-1939.

Fenner A.L. and Bull C.M. (2007). Short-term impact of grassland fire on the endangered pygmy bluetongue lizard. *Journal of Zoology* 272: 444-450.

Fox B.J. (1982). Fire and mammalian secondary succession in an Australian coastal heath. *Ecology* 63: 1332-1341.

Friend G.R. (1993). Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: a review. *Biological Conservation* 65: 99-114.

Funk W.C., Donnelly M.A. and Lips K.R. (2005). Alternative views of amphibian toe-clipping. *Nature* 433: 193.

Gamble T. (2010). A review of sex determining mechanisms in geckos (Gekkota: Squamata). *Sexual Development* 4: 88-103.

Godfrey S.S. and Hutchinson M.N. (2010). Notes on diet and reproductive condition of *Ctenotus* (Scincidae) of the mallee of South Australia. *Herpetofauna* 40: 2-8.

Gregory N.C., Sensenig R.L. and Wilcove D.S. (2010). Effects of controlled fire and livestock grazing on bird communities in east African savannas. *Conservation Biology* 24: 1606-1616.

Haslem A., Kelly L.T., Nimmo D.G., Watson S.J., Kenny S.A., Taylor R.S., Avitabile S.C., Callister K.E., Spence-Bailey L.M., Clarke M.F. and Bennett A.F. (2011). Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. *Journal of Applied Ecology* 48: 247-256.

Hawlena D., Saltz D., Abramsky Z. and Bouskila A. (2010). Ecological trap for desert lizards caused by anthropogenic changes in habitat structure that favor predator activity. *Conservation Biology* 24: 803-809.

Hines J.E. (1996). *RDSURVIV User's Manual.* Biological Resources Division, USGS. http://www.mbr-pwrc.usgs.gov/software/rdsurviv.html (accessed September 2011).

Hossack B.R., Eby L.A., Guscio C.G. and Corn P.S. (2009). Thermal characteristics of amphibian microhabitats in a fire-disturbed landscape. *Forest Ecology and Management* 258: 1414-1421.

Keith D.A. and Henderson M.K. (2002). Restoring the prepastoral condition: response to Jurskis. *Austral Ecology* 27: 691-693.

Keith D.A., Holman L., Rodoreda S., Lemmon J. and Bedward M. (2007). Plant functional types can predict decade-scale changes in fire-prone vegetation. *Journal of Ecology* 95: 1324-1337.

Kendall W.L. and Hines J.E. (1999). Program RDSURVIV: an estimation tool for capture-recapture data collected under Pollock's robust design. *Bird Study* 46: S32-S38.

Kendall W.L., Nichols J.D. and Hines J.E. (1997). Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78: 563-578.

Kendall W.L., Pollock K.H. and Brownie C. (1995). A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. *Biometrics* 51: 293-308.

Koch A.J. and Hero J.M. (2007). The relationship between environmental conditions and activity of the giant barred frog (*Mixophyes iteratus*) on the Coomera River, south-east Queensland. *Australian Journal of Zoology* 55: 89-95.

Laake J. and Rexstad E. (2008). RMark – an alternative approach to building linear models in MARK. In: *Program MARK: A Gentle Introduction, 7th Ed.* (eds. Cooch EG, White GC), pp. C1-C115. Available from: http://www.phidot.org/software/mark/docs/book/.

Langkilde T. and Shine R. (2006). How much stress do researchers inflict on their study animals? A case study using a scincid lizard, *Eulamprus heatwolei. The Journal of Experimental Biology* 209: 1035-1043.

Langlands P.R., Brennan K.E.C., Framenau V.W. and Main B.Y. (2011). Predicting the post-fire responses of animal assemblages: testing a trait-based approach using spiders. *Journal of Animal Ecology* 80: 558-568.

Le Galliard J.-F., Ferrière R. and Clobert J. (2005). Juvenile growth and survival under dietary restriction: are males and females equal? *Oikos* 111: 368-376.

Lebreton J.-D., Burnham K.P., Clobert J. and Anderson D.R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62: 67-118.

Lindenmayer D.B., Wood J.T., MacGregor C., Michael D.R., Cunningham R.B., Crane M., Montague-Drake R., Brown D., Muntz R. and Driscoll D.A. (2008). How predictable are reptile responses to wildfire? *Oikos* 117: 1086-1097.

Lyet A., Cheylan M., Prodon R. and Besnard A. (2009). Prescribed fire and conservation of a threatened mountain grassland specialist: a capture-recapture study on the Orsini's viper in the French alps. *Animal Conservation* 12: 238-248.

MacKenzie D.I., Nichols J.D., Sutton N., Kawanishi K. and Bailey L.L. (2005). Improving inferences in population studies of rare species that are detected imperfectly. *Ecology* 86: 1101-1113.

Moreira F., Catry F., Duarte I., Acácio V. and Silva J.S. (2009). A conceptual model of sprouting responses in relation to fire damage: an example with cork oak (*Quercus suber* L.) trees in southern Portugal. *Plant Ecology* 201: 77-85.

Moretti M., de Bello F., Roberts S.P.M. and Potts S.G. (2009). Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. *Journal of Animal Ecology* 78: 98-108.

O'Brien T.G., Kinnaird M.F., Nurcahyo A., Prasetyaningrum M. and Iqbal M. (2003). Fire, demography and the persistence of siamang (*Symphalangus syndactylus*: Hylobatidae) in a Sumatran rainforest. *Animal Conservation* 6: 115-121.

Olsson M., Wapstra E., Swan G., Snaith E., Clarke R. and Madsen T. (2005). Effects of long-term fox baiting on species composition and abundance in an Australian lizard community. *Austral Ecology* 30: 899-905.

Otis D.L., Burnham K.P., White G.C. and Anderson D.R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62: 1-135.

Pardon L.G., Brook B.W., Griffiths A.D. and Braithwaite R.W. (2003). Determinants of survival for the northern brown bandicoot under a landscape-scale fire experiment. *Journal of Animal Ecology* 72: 106-115.

Parr C.L. and Andersen A.N. (2006). Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Conservation Biology* 20: 1610-1619.

Petty A., Alderson J., Muller R., Scheibe O., Wilson K. and Winderlich S. (2007). *Arnhemland Plateau Draft Fire Management Plan.* Kakadu National Park. http://www.environment.gov.au/parks/publications/kakadu/fire-management-plan.html (accessed September 2011).

Pianka E.R. (1970). On *r*- and *K*-selection. *The American Naturalist* 104: 592-597.

Pike D.A., Webb J.K. and Shine R. (2010). Nesting in a thermally challenging environment: nest-site selection in a rock-dwelling gecko, *Oedura lesueurii* (Reptilia: Gekkonidae). *Biological Journal of the Linnean Society* 99: 250-259.

Pike D.A., Webb J.K. and Shine R. (2011). Removing forest canopy cover restores a reptile assemblage. *Ecological Applications* 21: 274-280.

Pollock K.H. (1982). A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46: 752-757.

Pollock K.H., Nichols J.D., Brownie C. and Hines J.E. (1990). Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107: 1-97.

Pradel R. (1996). Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52: 703-709.

R Development Core Team (2011). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Robinson A.C. and Heard M.B. (1985). National Parks. In: *Natural history of Eyre Peninsula.* (eds. Twidale CR, Tyler MJ, Davies M). Royal Society of South Australia, Adelaide, SA.

Sanz-Aguilar A., Anadón J.D., Giménez A., Ballestar R., Graciá E. and Oro D. (2011). Coexisting with fire: the case of the terrestrial tortoise *Testudo graeca* in mediterranean shrublands. *Biological Conservation* 144: 1040-1049.

Shine R. (1980). "Costs" of reproduction in reptiles. *Oecologia* 46: 92-100.

Smith A.L., Gardner M.G., Bull C.M. and Driscoll D.A. (2011). Primers for novel microsatellite markers in "fire-specialist" lizards (*Amphibolurus norrisi, Ctenotus atlas* and *Nephrurus stellatus*) and their performance across multiple populations. *Conservation Genetics Resources* 3: 345-350.

Specht R.L. (1972). *The Vegetation of South Australia.* AB James, Government Printer, Adelaide, SA.

Stanley T.R. and Richards J.D. (2005). Software review: a program for testing capture-recapture data for closure. *Wildlife Society Bulletin* 33: 782-785.

Templeton A.R., Robertson R.J., Brisson J. and Strasburg J. (2001). Disrupting evolutionary processes: the effect of habitat fragmentation on collared lizards in the Missouri Ozarks. *Proceedings of the National Academy of Science, USA.* 98: 5426-5432.

Twidale C.R. and Campbell E.M. (1985). The form of the land surface. In: *Natural history of Eyre Peninsula.* (eds. Twidale CR, Tyler MJ, Davies M). Royal Society of South Australia, Adelaide, SA.

Vernes K. and Haydon D.T. (2001). Effect of fire on northern bettong (*Bettongia tropica*) foraging behaviour. *Austral Ecology* 26: 649-659.

Warner D.A. and Shine R. (2009). Maternal and environmental effects on offspring phenotypes in an oviparous lizard: do field data corroborate laboratory data? *Oecologia* 161: 209-220.

Whelan R.J., Rodgerson L., Dickman C.R. and Sutherland E.F. (2002). Critical life cycles of plants and animals: developing a process-based understanding of population changes in fire-prone landscapes. In: *Flammable Australia: the fire regimes and biodiversity of a continent.* (eds. Bradstock RA, Williams JE, Gill AM). Cambridge University Press, Cambridge.

White G.C. (2005). Correcting wildlife counts using detection probabilities. *Wildlife Research* 32: 211-216.

White G.C. and Burnham K.P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* 46: 120-138.

Wilson S. and Swan G. (2008). *A Complete Guide to Reptiles of Australia*, 2 edn. New Holland, Sydney.

4.9 Supporting material

4.9.1 Captures and recaptures

Table S4.1 Number of initial captures (and recaptures) at each site in each primary session. No *Nephrurus stellatus* were captured in the late fire category at Hincks (HIL6 and HIL7).

	HINCKS				**PINKAWILLINIE**							
Primary session	**HIE1**	**HIE2**	**HIM1**	**HIM2**	**PE1**	**PE2**	**PM1**	**PM2**	**PL1**	**PL2**	**PL3**	**PL4**
SEASON 1												
1	5 (0)	4 (1)	12 (0)	5 (0)	1 (0)	1 (0)	5 (0)	5 (1)	0 (0)	0 (0)	1 (0)	1 (0)
2	2 (0)	9 (0)	16 (5)	13 (1)	2 (0)	2 (0)	2 (1)	2 (1)	0 (0)	0 (0)	1 (0)	0 (0)
3	2 (0)	0 (0)	1 (2)	1 (2)	2 (0)	6 (0)	9 (1)	9 (2)	0 (0)	0 (0)	1 (1)	1 (0)
SEASON 2												
4	27 (6)	45 (16)	49 (35)	38 (22)	8 (3)	5 (1)	9 (6)	11 (9)	0 (0)	0 (0)	0 (0)	0 (0)
5	7 (3)	7 (12)	11 (28)	15 (29)	5 (5)	9 (2)	8 (6)	7 (4)	2 (0)	1 (0)	0 (0)	0 (0)
6	6 (4)	13 (19)	7 (19)	13 (20)	4 (5)	4 (1)	6 (6)	4 (17)	0 (0)	4 (2)	0 (0)	1 (2)
TOTAL	49 (13)	78 (48)	96 (89)	85 (74)	22 (13)	27 (4)	39 (20)	38 (34)	2 (0)	5 (2)	3 (1)	3 (2)

4.9.2 Age, sex and reproductive status

4.9.2.1 Age and sex structure

The sex of all adult geckos was easily determined (see *4.3.2 Trapping protocol*), but juveniles were more difficult. The sex of female juveniles > 55 mm was sometimes apparent, as they mature at a larger size than males. Furthermore, we were sometimes able to assign a sex to juveniles post hoc when they were later recaptured. It was difficult to reliably estimate juvenile sex ratios as the assignment of a sex to a gecko varied between the sexes.

We used Fisher's exact tests to examine whether fire category influenced the age structure (ratio of juveniles to adults) and the sex ratio of *N. stellatus* populations (Table S4.2). Data from each season and location were analysed separately. There was no significant effect of fire category on age structure (P for all tests > 0.05), or sex ratios at the level of adults, juveniles, or the overall population (P for all tests > 0.14).

Data for these tests included all initial captures in each season, thus we also tested if the population structure changed over the course of each season using Fisher's exact tests on age or sex against primary session number. We found no significant effects of primary session on age structure (P for all tests > 0.15). There was also no effect of primary session on sex ratios (P for all tests > 0.16), except for juveniles at Hincks ($P = 0.02$ season one; $P < 0.001$ season two). This change in age structure of juveniles reflects the increase in our ability to determine juvenile sex at later stages in the season as they grew. Fewer geckos were scored as "unknown" in primary session three, than in primary session one. Furthermore, juvenile sex ratios became female-biased in the latter half of the season, as males reached maturity quickly. To determine if this change masked a fire effect, we tested each primary session in each season for fire effects on juvenile sex ratios at Hincks and none were significant (P for all Fisher's exact tests > 0.31). Although the sex ratios were generally male-biased, it is difficult to obtain reliable estimates given the large number of juveniles of unknown sex, and the different growth patterns between the sexes.

Table S4.2 Age and sex structure of *N. stellatus* in different fire categories.

Hincks

	Season 1		Season 2	
	Early	**Medium**	**Early**	**Medium**
Adult male	8	26	41	71
Adult female	6	6	24	28
Juvenile male	1	2	7	13
Juvenile female	2	10	19	25
Juvenile unknown	5	4	20	18

Pinkawillinie

	Season 1			Season 2		
	Early	**Medium**	**Late**	**Early**	**Medium**	**Late**
Adult male	8	15	4	25	24	4
Adult female	4	5	0	7	9	1
Juvenile male	0	0	0	1	4	0
Juvenile female	0	4	1	0	8	0
Juvenile unknown	2	8	0	6	10	3

4.9.2.2 Reproductive status

Females were only found to be gravid during the first primary trapping session of each season (November at Hincks and December at Pinkawillinie), never in January or February. We thus used Fisher's exact tests to examine fire effects on reproductive status in the first primary session only and included the initial capture only for each season (no within-season recaptures). In season two at Hincks, a higher proportion of gravid females was captured in the early than the medium fire category ($P = 0.01$) (Table S4.3). There was no effect of fire category on reproductive status at Pinkawillinie ($P = 1.00$) but the sample size was small (Table S4.3). There were not enough adult females captured in season one for reliable analysis (Table S4.3). Rainfall in the year prior to trapping was lower in season one than season two (Hincks = 251 and 377 mm; Pinkawillinie = 177 and 369 mm for season one and two, respectively) which may have contributed to the difference in fecundity between the seasons.

Table S4.3 Number of gravid adult female *N. stellatus*, compared with those not gravid in November (Hincks) and December (Pinkawillinie) of each season. * There was a significant effect of fire category on reproductive status at Hincks in season two (Fisher's exact test $P = 0.01$).

Hincks				
	Season 1		**Season 2 ***	
	Early	**Medium**	**Early**	**Medium**
Gravid	0	1	15	13
Not gravid	1	1	1	10
% gravid	0.0	50.0	93.8	56.5
% gravid/season		33.3		71.8

Pinkawillinie						
		Season 1			**Season 2**	
	Early	**Medium**	**Late**	**Early**	**Medium**	**Late**
Gravid	0	1	0	2	4	0
Not gravid	2	1	0	1	2	0
% gravid	0.0	50.0	NA	66.7	66.7	NA
% gravid/season			25.0			66.7

4.9.3 Fire effects on detectability

There was little support for effects of fire category group on capture probability. The best fitting models with group effects on capture probability had Akaike weights (w_i) of 0.091 at Hincks and 0.056 at Pinkawillinie (Table S4.4). While there was a strong relationship between capture probability and minimum temperature for these models, there was no significant difference between fire category groups (Fig. S4.1a). However, the lack of precision in the estimates for the late category at Pinkawillinie from low capture rates (Fig. S4.1b) may have masked an effect of fire on detectability.

Table S4.4 Candidate models for capture (p) and recapture (c) probability in *Nephrurus stellatus* at Hincks and Pinkawillinie. Models which included behaviour effects (p≠c) are indicated by (b). The global parameterisation for survival (S(sw+g)), abundance (N(sn+g)) and temporary emigration (γ”=γ’(.)) was used to investigate capture probability.

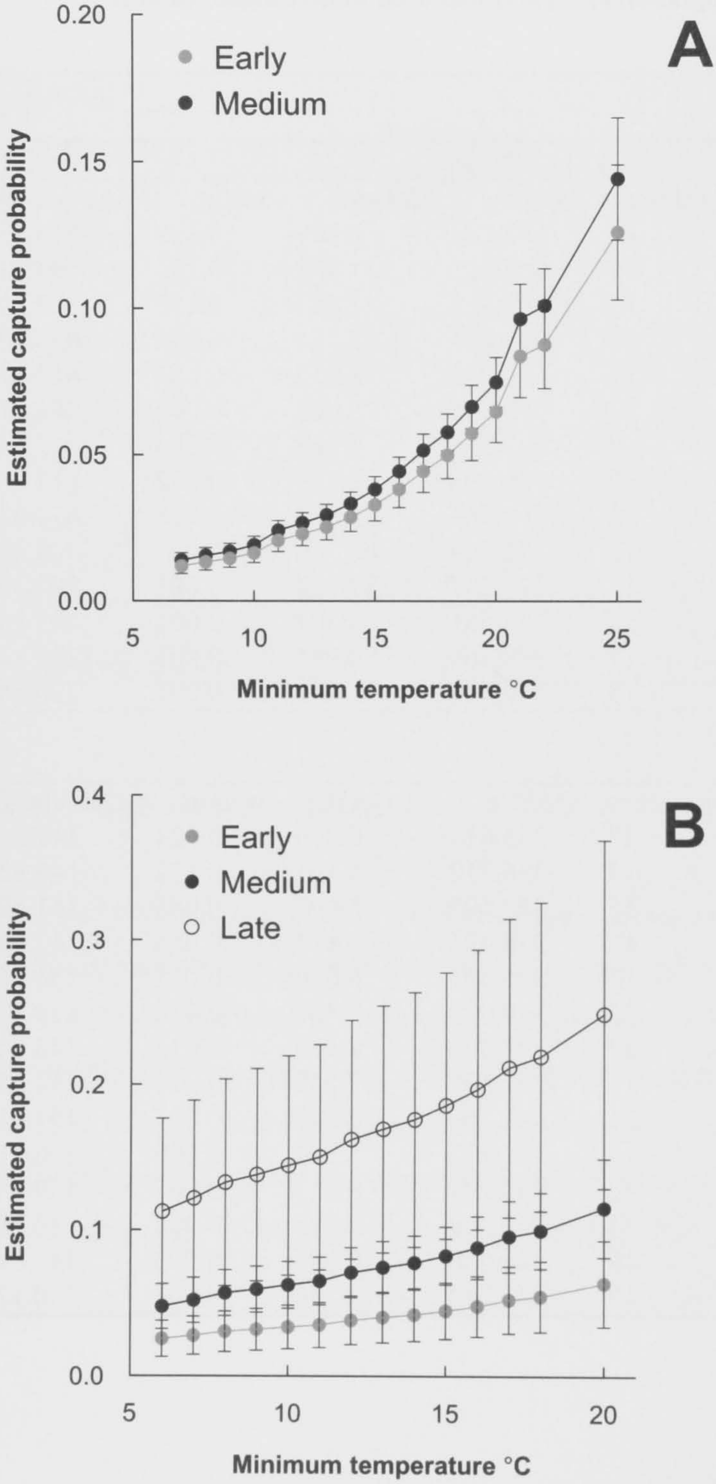
HINCKS

p and c	no. parameters	QAICc	Δ QAICc	weight	QDeviance
mt (b)	15	688.283	0.000	0.399	615.220
mt+sn (b)	25	689.521	1.238	0.215	594.818
mt	13	689.731	1.447	0.193	620.895
mt+g	14	691.234	2.951	0.091	620.289
mt+g (b)	17	691.935	3.652	0.064	614.611
mt+sn+g (b)	27	693.345	5.062	0.032	594.212
mt+sn	18	697.351	9.068	0.004	617.884
mt+sn+g	19	699.097	10.814	0.002	617.480
sn (b)	23	761.786	73.503	< 0.001	671.480
.	12	775.044	86.760	< 0.001	708.309
. (b)	13	775.937	87.654	< 0.001	707.101
g	13	776.681	88.397	< 0.001	707.845
sn	17	778.269	89.986	< 0.001	700.946
g (b)	15	779.719	91.436	< 0.001	706.656

PINKAWILLINIE

p and c	no. parameters	QAICc	Δ QAICc	weight	QDeviance
mt+sn (b)	27	333.612	0.000	0.624	117.858
mt (b)	17	336.712	3.101	0.132	145.937
mt	15	337.609	3.997	0.085	151.529
mt+g	17	338.424	4.812	0.056	147.649
.	14	340.431	6.820	0.021	156.663
sn (b)	25	340.918	7.306	0.016	130.371
mt+sn	20	341.040	7.429	0.015	143.042
g	16	341.169	7.557	0.014	152.753
mt+g (b)	21	341.769	8.157	0.011	141.313
. (b)	15	342.192	8.580	0.009	156.112
mt+sn+g	22	342.724	9.113	0.007	139.785
mt+sn+g (b)	31	342.905	9.293	0.006	116.395
sn	19	344.408	10.796	0.003	148.842
g (b)	19	345.742	12.130	0.001	150.176

Fig. S4.1 Estimates of capture probability (p) (± SE) from the best fitting models with fire category group effects for Hincks (A) and Pinkawillinie (B).



Chapter 5

Primers for novel microsatellite markers in "fire-specialist" lizards (*Amphibolurus norrisi*, *Ctenotus atlas* and *Nephrurus stellatus*) and their performance across multiple populations

Technical Note

Co-authors:
Michael G. Gardner
C. Michael Bull
Don A. Driscoll

I collected DNA samples from over 1300 lizards then developed molecular markers to study how fire affected their gene flow. (Photo C. Whitehead).

This chapter has been published:

Smith A.L., Gardner M.G., Bull C.M. and Driscoll D.A. (2011). Primers for novel microsatellite markers in "fire-specialist" lizards (*Amphibolurus norrisi*, *Ctenotus atlas* and *Nephrurus stellatus*) and their performance across multiple populations. *Conservation Genetics Resources* 3: 345-350.

5.1 Abstract

We developed 45 microsatellite markers for three lizard species with fire-related distributions: *Amphibolurus norrisi*, *Ctenotus atlas* and *Nephrurus stellatus* (17, 12 and 16 markers respectively). To isolate microsatellites we used an enrichment technique for *N. stellatus* and next-generation sequencing for *A. norrisi* and *C. atlas*. Fluorescent tags were attached to primers during PCR for flexible genotyping. All loci were polymorphic with 2-24 alleles and expected heterozygosities of 0.043-0.927. These markers will facilitate studies of post-fire dispersal and recolonisation.

5.2 Main text

Fire related distributions in many species are well documented but the processes behind these patterns are not, hindering predictions of the impact of fire regimes on biodiversity (Whelan et al. 2002). Fire-specialists (i.e. species which specialise on a specific post-fire stage) may become threatened if fire is not managed at appropriate scales. Dispersal affects post-fire recolonisation (Clarke 2008), and may critically influence how species respond to different fire regimes. Driscoll and Henderson (2008) identified a number fire-specialist Australian woodland reptiles including: *Nephrurus stellatus*, a burrowing gecko with an early successional response; *Ctentous atlas*, a spinifex specialist skink with a mid to late successional response; and the semi-arboreal agamid *Amphibolurus norrisi* whose fire response varied with location. We developed 45 novel microsatellite markers to study post-fire dispersal through analysis of gene flow in these three species.

A microsatellite library was constructed for *N. stellatus* using an enrichment technique on genomic DNA from liver tissue of two individuals (Australian Biological Tissue Collection, South Australian Museum (ABTC): 40819, 80029). We followed the protocol of Gardner et al. (2008) but hybridised the DNA with 3' Biotinylated oligos for AC and AAC microsatellite motifs (Murphy et al. 2009). We screened 128 insert positive clones (64 per motif) for microsatellites using the three primer PCR method of Gardner et al. (1999). We sequenced 64 clones (32 per motif) potentially containing microsatellites. MICROFAMILY 1.2 (Meglécz 2007) was used to remove redundant sequences and primers were designed for 32 microsatellites with suitable flanking regions.

Microsatellite libraries were compiled for *A. norrisi* and *C. atlas* using next-generation sequencing. Genomic DNA was extracted from liver tissue of two individuals of each species (ABTC: 80032, 53146 (*A. norrisi*) and 88779, 53770 (*C. atlas*)) and sequenced on a Roche 454 GS-FLX system at AGRF (www.agrf.org.au) with each sample occupying 12 % of a plate. The run produced 98,407 and 90,498 individual sequences of which 4.2 and 3.6 % contained microsatellites for *A. norrisi* and *C. atlas*, respectively. We used the program iQDD 0.9 (Meglécz et al. 2010) to identify sequences with a minimum of eight di-, tetra- or penta-base repeats, remove redundant sequences, and design primers for 39 *A. norrisi* and 32 *C. atlas* loci with PCR product lengths of 80-480 base pairs.

Multiplex-ready PCR tags were attached to the forward (5'-3': ACGACGTTGTAAAA) and reverse (5'-3': CATTAAGTTCCCATTA) primers (Hayden et al. 2008). After optimising primer concentrations (Table 5.1) we selected 21 (54 % of total screened) *A. norrisi*, 16 (50 %) *C. atlas*, and 18 (56 %) *N. stellatus* loci for genotyping using the method of Hayden et al. (2008). We amplified six loci in three duplex reactions (Table 5.1) and all other loci individually. PCR products were combined into two pools per species and genotyped on an ABI 3730 instrument (Applied Biosystems) with the size standard GS500 (-250) LIZ. We processed a total of 180 *A. norrisi*, 379 *C. atlas*, and 840 *N. stellatus* samples. We genotyped 8 % of samples on each plate twice to calculate scoring error rates per locus (Table 5.1) as the number of errors per number of alleles tested (DeWoody et al. 2006). Mean error rates were 2.1, 2.6 and 1.5 % for *A. norrisi*, *C. atlas* and *N. stellatus* respectively, which should not substantially bias estimates of population differentiation (Bonin et al. 2004). Two loci from each species failed to amplify consistently and were removed from the data set.

To assess the suitability of markers for analysis we used adult lizard genotype data from a target site within Hincks Conservation Park, South Australia. *N. stellatus* samples (N = 63) were collected from an area that last burnt in 1999 and *A. norrisi* (N = 23) and *C. atlas* (N = 54) samples were collected from an area that last burnt in 1966. For each locus we calculated the number of alleles, observed and expected heterozygosity using GENALEX 6.4 (Peakall & Smouse 2006), and deviation from Hardy-Weinberg

Equilibrium (HWE) using GENEPOP 3.4 (Raymond & Rousset 1995) (Table 5.2). *P* values from HWE tests were adjusted for multiple tests of significance using the sequential Bonferroni method (Hochberg 1988) (Table 5.2). We used MICROCHECKER 2.2.3 (Van Oosterhout et al. 2004) to check each locus for evidence of null alleles, scoring error due to stuttering, and large allele drop out. Six *A. norrisi* and four *C. atlas* loci showed significant null allele frequencies at the target site (Table 5.2). None of the loci showed evidence for large allele drop out, but one *A. norrisi* locus (AmNo02) showed evidence of scoring error due to stuttering consistent with our calculations (Table 5.1). We checked all pairs of loci in each species for linkage disequilibrium in GENEPOP and none were significant after sequential Bonferroni adjustment.

Because some loci showed deviation from HWE or null alleles, we analysed data from a number of additional sample sites to determine if these patterns were either locus or population specific. We used data from seven additional sample sites for *N. stellatus* (N = 23-48) and six additional sites for *A. norrisi* (N = 10-24) and *C. atlas* (N = 14-35). For each locus we calculated the percentage of comparison sites with evidence for a null allele and deviation from HWE (Table 5.2). Two loci each from *C. atlas* and *A. norrisi* failed both HWE and null allele tests at all sites and were removed from the data set leaving a final panel of 45 loci suitable for further research (Table 5.1, 5.2). These markers will enhance our ability to understand dispersal and implement fire management at scales appropriate for animals in fire-prone ecosystems.

5.3 Acknowledgements

This research was supported by funds from the Australian Research Council and the Government of South Australia's Wildlife Conservation Fund. Thanks for technical support go to Kathy Saint, Alison Fitch, Steve Donnellan and Terry Bertozzi at the South Australian Museum.

Table 5.1. Microsatellite primer sequences and locus information for the lizards *Amphibolurus norrisi*, *Ctenotus atlas*, and *Nephrurus stellatus*. Six *N. stellatus* loci were amplified in three duplex reactions, indicated by 1, 2 and 3.

Locus name	**GenBank accession no.**	**Forward primer sequence 5' - 3'**	**Reverse primer sequence 5' - 3'**	**Repeat motif**	**Size range (bp)**	**Primer conc. (Nm)**	**Fluorescent tag**	**Scoring error rate %**
Amphibolurus norrisi								
AmNo02	HQ283281	CAATGGTTTTCAGGAACTGGA	TTTGTCTCCTCCCTCCTTCC	$(AG)_{13}$	114 - 162	40	PET	6.3
AmNo04	HQ283282	TATTGTTCCCTCCCCTTCCT	GGGTTGCAGGGATTTGTTAG	$(AT)_{9}$	137 - 157	10	VIC	0.0
AmNo05	HQ283283	TAACCGACTGGATAGGCGAG	TGGTTTTGAATCATTGCTGC	$(AAAC)_{12}$	106 - 146	40	NED	7.1
AmNo11	HQ283285	GCCATTAACTGTGCTGGCTT	TTTCTAACATAACTACTGCACAGCAA	$(AG)_{16}$	167 - 231	40	PET	0.0
AmNo12	HQ283286	TCCTGATGAGGATGAGGAGG	CTCCAGTTGCACAGCAACAC	$(AC)_{10}$	162 - 208	20	NED	0.0
AmNo18	HQ283287	AAAACAGCACTGTATCTTTCAATTT	AAATGAGTTTGGGGCATGAG	$(AC)_{14}$	238 - 278	20	VIC	6.3
AmNo20	HQ283288	GCCCACAACAGAAGTTTTGC	GGCTGGACTCCTGGTTATCA	$(AG)_{12}$	233 - 253	60	NED	0.0
AmNo24	HQ283290	CAGACCAGATAGGCGGGATA	CCATAAGTTCCACCGATTCAA	$(AAAT)_{16}$	222 - 342	20	FAM	0.0
AmNo25	HQ283291	AAGAAGTGCCAGGCCACC	GGTGTGTTTTCCATTTGCTG	$(AG)_{8}$	311 - 321	10	NED	0.0
AmNo26	HQ283292	TGGTTCCAGAGTGCCTCATT	TGTTCCTCTTTGGACCAACC	$(AC)_{11}$	316 - 332	40	NED	0.0
AmNo29	HQ283293	GGGCCTACTTTGTGACTTGC	TTGACTAGATAGGACGGGTAACAA	$(AAAT)_{18}$	264 - 378	20	FAM	0.0
AmNo30	HQ283294	GTTTCCTTTCCCTTTCCCAA	AAGGCACAATGGCTGAAATC	$(AAAT)_{13}$	288 - 380	40	PET	0.0
AmNo31	HQ283295	TGAAACCAGATCTTCTCAAAAGG	CCAATCCATTTCTAGGACCA	$(AAAT)_{13}$	294 - 402	10	PET	16.7
AmNo33	HQ283296	CAACAAAACTAAATCTTAGTGGCA	CGTTGCCTTGAGGGTGTATAA	$(AC)_{11}$	418 - 430	20	NED	0.0
AmNo36	HQ283297	CAGACATTTTCCAACTTTTAAGGA	GCAGACAAAAGACTCGTCTGAA	$(AATG)_{10}$	459 - 571	20	VIC	0.0
AmNo37	HQ283298	CAGTCATTTAGGATACTGGGAATG	TCAAATACAATCTAAAGTCTATTGCAG	$(AAAT)_{10}$	420 - 504	10	FAM	0.0
AmNo39	HQ283299	TGCAGTTGAATGTTTAAGGGTT	GCTTAGTCAATCCTATCCATTTCC	$(AAAT)_{16}$	392 - 480	60	VIC	0.0
Ctenotus atlas								
CtAt01	HQ283300	AAACCCGAAAGCATGATGAG	GTCAGCACCTTGAATGCAAAT	$(AG)_{13}$	93 - 135	10	FAM	5.6
CtAt02	HQ283301	ATGAAATGCTTACGCAGACG	TTGACAAAAGGGCAATGTAGG	$(AC)_{14}$	117 - 159	20	FAM	0.0
CtAt03	HQ283302	TCAAACAAGGAATTATTGTTCATTACA	GCAAACCAGTCTTGTCTGGTAAA	$(AG)_{10}$	116 - 168	10	NED	7.9
CtAt04	HQ283303	TCAATCCTCAGTTGCCTCCT	TGCCTGTATTATTTCATGCCAA	$(AAGT)_{13}$	101 - 173	20	NED	0.0
CtAt08	HQ283304	TATCAGTAACGCAGTCGCGG	ACTTCGGACCAAACCTCCTT	$(AG)_{8}$	177 - 199	20	VIC	1.9
CtAt09	HQ283305	GTTGGCTGTAAACCCAGCAT	CCTCTTCAAAGCCAAGCATC	$(AG)_{8}$	162 - 194	10	PET	0.0
CtAt12	HQ283306	TGTTAGAGACGGAACTTTGATGA	CTCTAAGGGTGTGGTGCGTT	$(AATG)_{14}$	141 - 205	20	PET	0.0
CtAt15	HQ283307	CCCTTGTGCTGGTGAAACTT	TGCGCTCAGCAAATGTAATC	$(AATG)_{8}$	254 - 311	10	NED	1.7
CtAt18	HQ283308	GATGAAGCTCAGGAAGCCAG	TACATGGCCACTTTGCTGAA	$(AC)_{11}$	346 - 396	20	PET	0.0
CtAt20	HQ283309	CTCCACGACTTCCTCACCAT	ATGATCCAGATTACCGGTCG	$(AC)_{8}$	308 - 368	20	VIC	4.5
CtAt24	HQ283311	GCTACCTGCATCGCTGTTG	TTCTGGAAGACTGTGGCTCC	$(ACAG)_{11}$	325 - 389	10	NED	0.0
CtAt30	HQ283312	AGCCATTGCTACATGCTGTG	CAGCCAACGTTGTCCCTA	$(AAGT)_{16}$	377 - 445	20	VIC	10.0

Locus name	GenBank accession no.	Forward primer sequence 5' - 3'	Reverse primer sequence 5' - 3'	Repeat motif	Size range (bp)	Primer conc. (Nm)	Fluorescent tag	Scoring error rate %
Nephrurus stellatus								
NeSt05[1]	HQ283314	TGCATTATCTAGTTGTGGACTG	CACTGCTCATGGTAACACAC	$(TG)_{20}$	142 - 172	20	VIC	3.2
NeSt06	HQ283315	CATGTGTTCACACACTTACACAC	GTCTGTGGTCTCTTGCTGG	$(AC)_{19}$	97 - 137	20	NED	0.8
NeSt09[1]	HQ283316	TAAGATCACAGCACCTGAGC	TTCCATTGCCTATTTCCG	$(AAC)_6A(AAC)_4$	225 - 267	20	VIC	0.0
NeSt11[2]	HQ283317	CATCAGTGAATCCCTGCTG	CGATTCTCAGCAAACACAC	$(TG)_{24}$	294 - 330	20	NED	0.0
NeSt16	HQ283318	ACCCTTCTCTTGATGAGGTG	TTAAGGAAGACAGCTTGCC	$(AC)_{24}$	215 - 259	40	FAM	2.3
NeSt18[3]	HQ283319	CCCGTGTTGCCATATTAAG	CAAAACACCTCAATCATTGC	$(GT)_{25}$	108 - 146	20	FAM	1.4
NeSt23[3]	HQ283320	AGGGTCAGGTGACACAGTATC	CATTTAATAGTGGCATGACATC	$(TG)_{22}$	208 - 246	20	FAM	0.7
NeSt28	HQ283321	ACCAATTCAATCATAGGATCAC	ACAGCCTAACATACATCACAAG	$(GTT)_{27}$	230 - 287	20	VIC	1.4
NeSt31	HQ283322	AAGCTGCCTTGAGATATTATG	GAGAGTAGCATGGGACGAAC	$(TTC)_{10}TCC$ $(TTC)_5(N)_{18}$ $(TCC)_4(TTG)_{17}$ $(TTC)_{22}$	293 - 383	20	FAM	2.6
NeSt32	HQ283323	GAGTTCACAATTACCCAGACAG	TAATTCCAATAGAACACAGCG	$(TTG)_{15}$	278 - 311	20	PET	5.5
NeSt33	HQ283324	GCCATCTGTTTGAGACTATTG	AGAATCCAGCTTGGAGTCTAG	$(ATT)_9(GTT)_{15}$	214 - 262	20	PET	0.0
NeSt35	HQ283325	ACTGAATGAAGTGAGACATAAGTC	AACGTGCCTCCTCCTCAC	$(AAC)_{11}$	197 - 241	20	NED	0.0
NeSt38	HQ283326	CACCAACAAGGCAAATAGC	TCCTTTCTGGATTGTGTGG	$(GTT)_{17}$	289 - 349	20	NED	2.0
NeSt43	HQ283327	GTGATGGCATCATCCTCAG	AGCAGCAGCCTGACTCTG	$(GTT)_{14}$	154 - 220	20	PET	0.0
NeSt46	HQ283328	CTGTCCTCAACAGCTAGTGC	AAGCCTAACAGTGCTATTCTAAG	$(GTT)_{13}$	270 - 303	20	PET	2.0
NeSt47[2]	HQ283329	GATCTTGAATGACATCGTGC	CTCTTCTGCATTAGTCTGAGTTC	$(CAA)_{17}$	193 - 253	20	NED	2.1

Table 5.2. Population statistics for microsatellite markers in the lizards *Amphibolurus norrisi*, *Ctenotus atlas*, and *Nephrurus stellatus*.

	Target sample site					Comparison sample sites	
Locus name	**No. alleles**	H_O	H_E	P	**Freq. null alleles**	**% sites with HW disequilibrium**	**% sites with null allele**
***Amphibolurus norrisi* (target site N = 23, no. comparison sites = 6)**							
AmNo02	10	0.476	0.771	< 0.001*	0.194†	17	33
AmNo04	6	0.826	0.808	0.945	-0.009	0	0
AmNo05	8	0.826	0.821	0.501	-0.009	0	0
AmNo11	12	0.682	0.781	0.096	0.073	0	0
AmNo12	6	0.600	0.666	0.092	0.039	0	33
AmNo18	11	0.652	0.836	0.036	0.113†	0	50
AmNo20	7	0.609	0.664	0.209	0.048	0	0
AmNo24	18	0.739	0.913	0.043	0.096†	83	83
AmNo25	5	0.545	0.655	0.062	0.096	17	0
AmNo26	6	0.818	0.693	0.634	-0.123	0	0
AmNo29	17	0.850	0.915	0.006	0.033	17	0
AmNo30	18	0.783	0.925	< 0.001*	0.079†	0	0
AmNo31	14	0.643	0.885	0.001*	0.140†	50	67
AmNo33	2	0.043	0.043	0.915	-0.022	17	17
AmNo36	17	0.783	0.926	0.004	0.077†	0	17
AmNo37	15	0.864	0.916	0.566	0.030	17	33
AmNo39	15	0.909	0.895	0.591	-0.008	0	0
***Ctenotus atlas* (target site N = 54, no. comparison sites = 6)**							
CtAt01	12	0.510	0.751	< 0.001*	0.158†	33	83
CtAt02	6	0.519	0.557	0.036	0.041	0	0
CtAt03	21	0.902	0.905	0.543	0.003	0	0
CtAt04	12	0.522	0.838	< 0.001*	0.187†	33	100
CtAt08	9	0.756	0.852	0.035	0.054	0	0
CtAt09	8	0.740	0.734	0.954	-0.004	0	0
CtAt12	14	0.827	0.885	0.666	0.032	0	0
CtAt15	24	0.884	0.925	0.052	0.025	0	17
CtAt18	8	0.653	0.742	0.559	0.065	0	0
CtAt20	15	0.647	0.884	< 0.001*	0.137†	50	50
CtAt24	12	0.875	0.902	0.716	0.015	0	0
CtAt30	14	0.744	0.883	0.114	0.079†	33	33
***Nephrurus stellatus* (target site N = 63, no. comparison sites = 7)**							
NeSt05	11	0.831	0.878	0.440	0.028	29	57
NeSt06	14	0.949	0.878	0.946	-0.043	0	0
NeSt09	14	0.836	0.852	0.214	0.009	0	0
NeSt11	22	0.857	0.880	0.107	0.016	0	0
NeSt16	13	0.839	0.845	0.631	0.006	0	0
NeSt18	15	0.852	0.900	0.407	0.029	14	0
NeSt23	15	0.885	0.875	0.511	-0.007	0	0
NeSt28	13	0.787	0.730	0.923	-0.084	0	14
NeSt31	20	1.000	0.927	0.766	-0.040	0	0
NeSt32	10	0.695	0.773	0.371	0.047	14	43
NeSt33	14	0.885	0.898	0.514	0.007	0	0
NeSt35	15	0.755	0.766	0.738	0.001	0	0
NeSt38	15	0.857	0.887	0.552	0.017	0	0
NeSt43	11	0.870	0.855	0.780	-0.011	0	0
NeSt46	10	0.847	0.782	0.608	-0.042	0	0
NeSt47	15	0.803	0.872	0.083	0.042	0	0

Observed (H_O) and expected (H_E) heterozygosity, probability value from Hardy-Weinberg equilibrium test (P). * significant Hardy-Weinberg disequilibrium after sequential Bonferroni adjustment, † presence of a null allele.

5.4 References

Bonin A., Bellemain E., Bronken Eidesen P., Pompanon F., Brochmann C. and Taberlet P. (2004). How to track and assess genotyping errors in population genetics studies. *Molecular Ecology* 13: 3261-3273.

Clarke M.F. (2008). Catering for the needs of fauna in fire management: science or just wishful thinking? *Wildlife Research* 35: 385-394.

DeWoody J., Nason J.D. and Hipkins V.D. (2006). Mitigating scoring errors in microsatellite data from wild populations. *Molecular Ecology Notes* 6: 951-957.

Driscoll D.A. and Henderson M.K. (2008). How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model. *Biological Conservation* 141: 460-471.

Gardner M.G., Cooper S.J.B., Bull C.M. and Grant W.N. (1999). Isolation of microsatellite loci from a social lizard, *Egernia stokesii*, using a modified enrichment procedure. *The Journal of Heredity* 90: 301-304.

Gardner M.G., Sanshez J.J., Dudaniec R.Y., Rheinberger L., Smith A.L. and Saint K.M. (2008). *Tiliqua rugosa* microsatellites: isolation via enrichment and characterisation of loci for multiplex PCR in *T. rugosa* and the endangered *T. adelaidensis*. *Conservation Genetics* 9: 233-237.

Hayden M.J., Nguyen T.M., Waterman A. and Chalmers K.J. (2008). Multiplex-Ready PCR: A new method for multiplexed SSR and SNP genotyping. *BMC Genomics* 9: 80.

Hochberg Y. (1988). A sharper Bonferroni procedure for multiple tests of significance. *Biometrika* 75: 800-802.

Meglécz E. (2007). MICROFAMILY (version 1): a computer program for detecting flanking-region similarities among different microsatellite loci. *Molecular Ecology Notes* 7: 18-20.

Meglécz E., Costedoat C., Debut V., Gilles A., Malausa T., Pech N. and Martin J.-F. (2010). QDD: a user-friendly program to select microsatellite markers and design primers from large sequencing projects. *Bioinformatics* 26: 403-404.

Murphy A.R., Gardner M.G. and Fox S.F. (2009). Isolation of microsatellites via enrichment and a sequence tagged method in a South American lizard with suspected parental care, *Liolaemus leopardinus*. *Conservation Genetics Resources* 1: 13-16.

Peakall R. and Smouse P.E. (2006). GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* 6: 288-295.

Raymond M. and Rousset F. (1995). GENEPOP (Version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity* 86: 248-249.

Van Oosterhout C., Hutchinson W.F., Wills D.P.M. and Shipley P. (2004). MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes* 4: 535-538.

Whelan R.J., Rodgerson L., Dickman C.R. and Sutherland E.F. (2002). Critical life cycles of plants and animals: developing a process-based understanding of population changes in fire-prone landscapes. In: *Flammable Australia: the fire regimes and biodiversity of a continent.* (eds. Bradstock RA, Williams JE, Gill AM). Cambridge University Press, Cambridge.

Chapter 6

Dispersal across fire mosaics in a "fire specialist" knob-tailed gecko

Research Paper

Co-authors:
C. Michael Bull
Michael G. Gardner
Don A. Driscoll

This open, sandy area in Hincks Wilderness Area that last burnt in 1999 is prime habitat for the knob-tailed gecko, Nephrurus stellatus. *(Photo: A.L. Smith, taken Nov 2009 at the site "HIM1").*

6.1 Abstract

Patchy habitats affect dispersal in many animal species, but few studies have examined how dispersal varies across fire mosaics, meaning the effect of fire management actions on population connectivity is largely unknown. We studied dispersal in a "fire specialist" gecko, *Nephrurus stellatus*, that is common (up to 50 / ha) in habitats with 5-10 years since fire and rare (< 4 / ha) in habitats with > 30 years since fire. Using a combination of microsatellite DNA and mark-recapture data, we asked whether gene flow, genetic diversity and movement rates declined with increasing fire in the landscape (characterised by time since fire and fire frequency). We replicated our study regionally in four reserves consisting of mallee vegetation with complex fire mosaics. Bayesian clustering analyses identified genetic differentiation among the reserves, but there was no genetic structure within reserves, indicating high gene flow. At the location where our sample size was largest, analysis of landscape resistance revealed higher gene flow in recently burnt, and more frequently burnt habitats. At another reserve we found significant isolation by distance, and lower gene flow at higher elevations. Among all reserves, genetic diversity declined significantly with increasing time since fire. The distance that geckos moved per day also declined significantly with time since fire. The maintenance of high gene flow within reserves may reflect an adaptation to its temporally dynamic habitat, but our results suggest that post-fire succession can restrict dispersal in *N. stellatus*. Fire management plans that incorporate information about animal dispersal are likely to have a greater chance of conserving biodiversity because they will allow species to maintain population connectivity and adaptive potential.

6.2 Introduction

Dispersal is a key life-history parameter influencing the persistence of species in fragmented landscapes (Thomas 2000; Travis 2003; Schtickzelle et al. 2006). The ability for animals to disperse between patches of habitat is critical for maintaining gene flow and genetic diversity (Frankham 1997; Saccheri et al. 1998), and for enabling recolonisation following local extinction (Hanski 1998). Many studies have demonstrated that habitat fragmentation by human activity has strongly restricted animal dispersal (Banks et al. 2005; Levy et al. 2010; Driscoll et al. 2012b; Lange et al.

2012). Different vegetation types within a landscape also form natural habitat mosaics which can influence dispersal of species that specialise on a particular vegetation type (Schooley & Wiens 2004; Bates et al. 2006; Wilson et al. 2009). For example, species that live in rocky outcrops within grasslands or woodlands often have strong genetic structure that reflects the natural patchiness of their habitat (Stow et al. 2001; Berry et al. 2005; Piggott et al. 2006). However, spatial patchiness in vegetation structure is also generated in relatively uniform habitats through disturbance and succession (White & Pickett 1985). Little is known about how dispersal varies among connected patches of the same vegetation type, that differ only in their successional development.

In fire-prone ecosystems, many animal species are "fire specialists" that are adapted to habitat that develops at a particular stage after fire, so their local abundance is affected by succession (Driscoll & Henderson 2008). Different fire specialists reach their peak abundance at different times after fire, meaning that community structure changes with habitat succession (e.g. Moretti et al. 2009). To cater for these changes, management agencies often use prescribed burning and/or fire suppression to create a "fire mosaic" under the assumption that successional diversity in vegetation will benefit biodiversity more broadly (Parr & Andersen 2006; Cushman et al. 2008). However, the spatial and temporal scales at which fire mosaics should be maintained has been quantified for very few animal species (Bradstock et al. 2005; Clarke 2008). For fire specialists, inappropriate fire regimes can fragment populations if dispersal ability is influenced by successional changes in habitat structure (Templeton et al. 2011). For example, late successional vegetation may form a barrier to dispersal for species which specialise on recently burnt habitats. If the spatial scale of an unfavourable fire mosaic is large enough to restrict gene flow, genetic diversity may decline, reducing the fitness and adaptive potential of isolated populations (Templeton et al. 2001). Quantifying the effect of succession on dispersal is therefore critical to determine how fire regimes will influence the connectivity of fire specialist animal populations (Clarke 2008; Driscoll et al. 2010).

There has been progress towards understanding short-term effects of fire on animal dispersal through spatial patterns of recolonisation (Brotons et al. 2005; Knight & Holt 2005; do Rosário & da Luz Mathias 2007; Murphy et al. 2010b; Banks et al. 2011) but the long-term effects of post-fire succession on dispersal are less understood. Recent studies have begun addressing this knowledge gap using molecular data to examine successional changes in gene flow (Stow et al. 2007; Murphy et al. 2010a; Spear & Storfer 2010; Schrey et al. 2011). Genetic data can be ideal for this purpose because they incorporate the effects of recruitment and long-distance dispersal which is rarely documented through direct observation (Broquet & Petit 2009). Consequences of dispersal variation on population fitness can also be inferred by analysing successional changes in genetic diversity (Schrey et al. 2011). Furthermore, analysis of landscape genetic structure can be used to examine the relative importance of permanent landscape features such as elevational gradients (Cushman et al. 2006; Murphy et al. 2010a). Application of genetic data to fire ecology therefore has huge potential, but also has limitations. Fire can have instant and profound effects on populations resulting from displacement (Banks et al. 2012) and direct mortality (Griffiths & Christian 1996). Untangling the ongoing effects of habitat succession on dispersal with residual genetic signals from an initial impact may be difficult with genetic data alone (Driscoll & Hardy 2005). Combining analyses of gene flow with direct measures of movement can avoid the limitations of either method used separately (Cushman & Lewis 2010; Leidner & Haddad 2011). This may provide the most informative picture of how habitat succession affects dispersal.

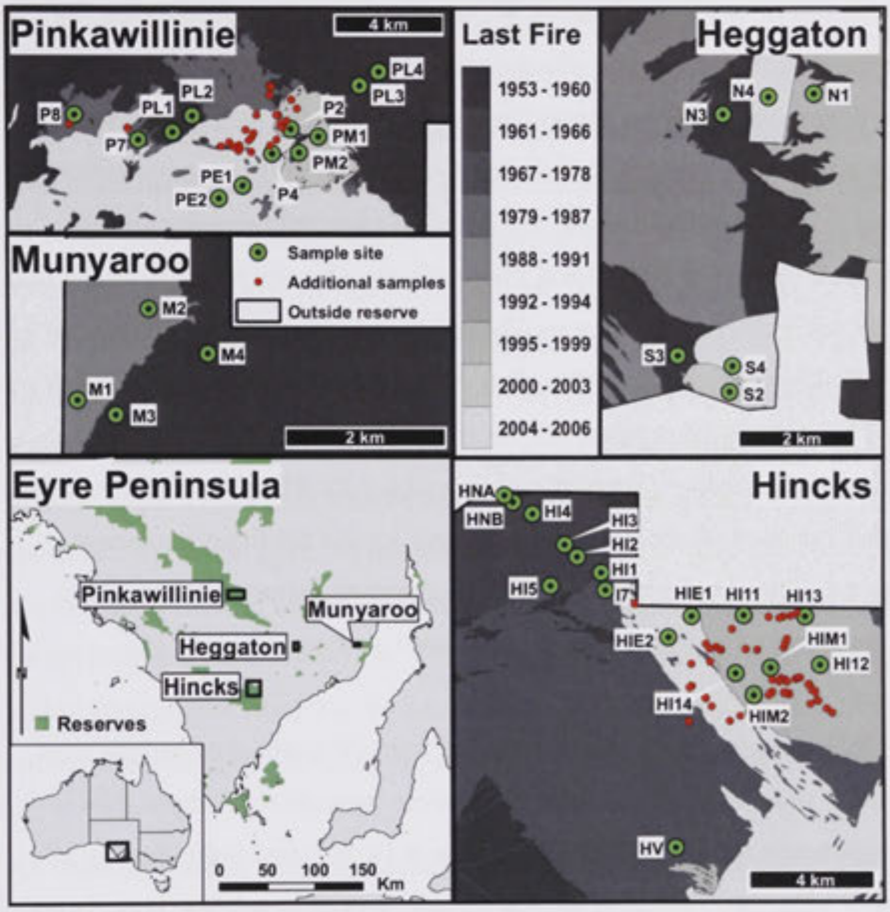
In this study we combined microsatellite DNA and mark-recapture data to examine movement, gene flow and genetic diversity in a fire specialist Australian knob-tailed gecko, *Nephrurus stellatus*. Following fire, the population density of this species increases markedly towards a peak in abundance (up to 50 individuals / ha) at 5-10 years after fire (Driscoll et al. 2012a; Smith et al. 2012). This is followed by a sharp decline in density, such that *N. stellatus* is rare (less than 4 / ha) in habitats with more than 30 years since fire (Driscoll et al. 2012a; Smith et al. 2012). Our aim was to investigate if this population decline was associated with changes in dispersal. We asked if increasing time since fire corresponded to variation in movement, gene flow and genetic diversity in *N. stellatus*. To address this question, we took three approaches. First, we analysed genetic population structure within four replicate landscapes. Recurrent fire promoted succession mosaics of the same vegetation type in all of our study landscapes, enabling us to examine variation in dispersal across the mosaics. Using landscape resistance analyses, we assessed the relative importance of fire mosaics (characterised by time since fire and fire frequency), topography, and population density on gene flow in *N. stellatus*. Second, we investigated if successional changes in vegetation were associated with variation in genetic diversity. Third, we conducted mark-recapture surveys to determine if daily movement rates of geckos differed among habitats with increasing time since fire.

6.3 Methods

6.3.1 Study region & species

The study took place in four conservation reserves on the Eyre Peninsula, South Australia (Fig. 6.1): Hincks Wilderness Area (33°45' S, 136°03' E; 66,658 ha), Pinkawillinie Conservation Park (32°54' S, 135°53' E; 130,148 ha), Munyaroo Conservation Park (33° 21' S, 137° 12' E; 20,139 ha), and Heggaton Conservation Reserve (33°22' S, 136°31' E; 6,476 ha). The region is semi-arid, with an average annual rainfall of 340 mm at Hincks, 303 mm at Pinkawillinie, 296 mm at Munyaroo, and 361 mm at Heggaton. The main topographic features are white sand dunes, occurring in either large, parabolic fields or longitudinal ridges, interspersed by hard, reddish-brown swales (Twidale & Campbell 1985). The reserves are dominated by mallee vegetation which is characterised by multi-stemmed *Eucalyptus spp*., predominantly *E. costata*, and *E. socialis*, associated with the shrubs *Melaleuca uncinata*, *Callitris verrucosa* and the spiky hummock grass *Triodia irritans* (Specht 1972; Robinson & Heard 1985). Summer lightning is the most common ignition source of mallee which typically results in large, severe wildfires on a decadal time scale (Bradstock & Cohn 2002).

Fig. 6.1. *Nephrurus stellatus* was studied across fire mosaics in four conservation reserves on the Eyre Peninsula, South Australia. The green circles are sample sites and the red circles are locations where additional individual samples were collected between the sample sites.



Nephrurus stellatus is distributed widely across the Eyre Peninsula and in a small area of central-south Western Australia (Wilson & Swan 2010). Higher abundance of *N. stellatus* in recently burnt (5-10 years after fire) than long unburnt (> 18 years after fire) mallee occurs consistently at four different conservation reserves on the Eyre Peninsula (Driscoll & Henderson 2008), and reflects changes in population density rather than detectability (Smith et al. 2012). *Nephrurus stellatus* is common in sandy areas, residing in self-dug burrows by day and actively foraging for invertebrate prey by night (Cogger 1996). Preliminary skeletochronological analysis suggests that *N. stellatus* can live for at least four years in the wild (A. Smith, unpublished data). Males can reach sexual maturity in their first year, and females have been found gravid in their second year (A. Smith, unpublished data).

6.3.2 Overview of study design

We collected a total of 764 *N. stellatus* DNA samples across fire mosaics in the four reserves (Hincks = 494, Pinkawillinie = 216, Munyaroo = 32, and Heggaton = 22; Fig. 6.1). The samples were used to quantify gene flow in a series of genetic structure and landscape resistance analyses (details below). We analysed gene flow among the four reserves to understand the broad genetic structure, but we focussed predominantly on quantifying gene flow within reserves across fire mosaics. The samples were also used to analyse variation in genetic diversity across fire mosaics. To directly study movement rates, we used data from 109 individual geckos that were captured more than once during mark-recapture surveys at Hincks and Pinkawillinie. Our DNA sample collection took place over six consecutive field seasons (the spring/summer period when lizards in the mallee are most active), from Dec 2004 – Feb 2005 (season 1) to Nov 2009 – Feb 2010 (season 6). The majority of samples (93 %) and the mark-recapture data were collected in the final three seasons (Supporting material 6.8.1). All of the DNA samples were collected after the most recent fire in each reserve, except for three samples at Heggaton that were collected before fires in 2006 (Supporting material 6.8.1). These three samples were removed for the landscape resistance analyses.

The majority of DNA samples (90 %) were collected from 39 established sample sites (Fig. 6.1). Additional samples were collected in the areas between the sample sites to achieve a more continuous sampling distribution (Fig. 6.1). We used individual-level analyses to quantify gene flow, avoiding arbitrary definitions of population boundaries. This approach was particularly suitable for our study because individual-level landscape genetics analysis can detect effects on gene flow from recently established (1-15 generations) landscape barriers (Landguth et al. 2010) such as those potentially created by fire and vegetation succession. We collected DNA samples at spatial scales relevant to natural and prescribed fires in the mallee (Bradstock & Cohn 2002) and relevant to commonly reported extents of genetic structure in lizards (Stow et al. 2001; Sumner et al. 2001; Berry et al. 2005; Hoehn et al. 2007; Smith et al. 2009). The mean (and range) distance between individual samples within reserves was 3.2 (0-13.8) km at Hincks, 3.2 (0-12.0) km at Pinkawillinie, 1.0 (0-2.0) km at Munyaroo, and 2.9 (0-5.6) km at Heggaton (Fig. 6.1). At these scales, we collected DNA samples from areas spanning 0.7 to 57 years after fire (Fig. 6.1, Supporting material 6.8.1). Hincks had a more complex fire history than the other three reserves, meaning our sample sites also spanned a greater range of fire frequencies (0-5 fires since 1953, Supporting material 6.8.1).

6.3.3 Field data & sample collection

Thirty-two of the 39 sample sites consisted of pitfall trap stations arranged in either transects (15 sites) or grids (17 sites) (Supporting material 6.8.1). The transect sites had 22 pitfall traps arranged in pairs at 40 m intervals along a 400 m transect, with a 20 m drift fence intersecting each trap pair (Driscoll & Henderson 2008). The grid sites had 25 pitfall traps in a 1 ha grid, with five rows of five traps spaced at 25 m intervals, each intersected by a 10 m drift fence (Smith et al. 2012). Traps consisted of a 20 litre bucket buried flush with the ground surface. Trapped animals could shelter in a half PVC pipe placed at the bottom of each bucket and covered with a wood block which also acted as a floating refuge in case of heavy rain. In each season, during three 5-15 day trap periods, traps within each reserve were opened and closed at the same times and checked daily while open. At the remaining seven sites, geckos were captured manually after locating them at night (Supporting material 6.8.1). The areas covered by these sites varied from 0.05 to 15 ha (mean = 6.7) and the distance between captured animals within sites ranged from 0 to 917 m (mean = 210). The additional individual samples collected between the sample sites were also collected manually at night.

All captured geckos were measured (snout-vent length), weighed and the sex of adults was determined by external hemipenal bulges, present in males but not females. Geckos were recorded as adult or juvenile based on size to sexual maturity (Smith et al. 2012). For initial captures, a single toe tip from the back foot was clipped as a batch mark, unique to each season (Funk et al. 2005). For the grid sites and manual captures a small amount of blood from the toe was stored on FTA paper (Whatman) as a DNA source. Tissue from the clipped toe was preserved as an additional DNA source in liquid nitrogen or 5 ml ethanol/physiological saline (1:1). We used a Visible Implant Elastomer kit (Northwest Marine Technology) to apply a unique visual mark to each gecko under the ventral skin surface. This allowed us to reliably identify individuals upon recapture (Smith et al. 2012) and determine the distance moved since their previous capture. Data from the grid sites only were used in the movement analysis. Pitfall trapped animals were taken to a base for processing and released the following day, 5 – 10 m from the capture location. Manually captured animals were processed and released immediately.

6.3.4 Microsatellite data

We extracted DNA from FTA paper following Smith and Burgoyne (2004). Where FTA samples were not available, DNA was extracted from the tissue sample using a modified Gentra kit (Qiagen). We amplified a panel of 14 microsatellite markers (NeSt06, NeSt09, NeSt11, NeSt16, NeSt18, NeSt23, NeSt28, NeSt31, NeSt33, NeSt35, NeSt38, NeSt43, NeSt46, NeSt47) which had previously reported low rates of Hardy-Weinberg (HW) disequilibrium and null alleles across multiple sample sites (Smith et al. 2011). Samples were genotyped on an ABI 3730 instrument (Applied Biosystems) with the size standard GS500 (-250) LIZ and alleles were scored with GeneMapper 4.0 (Applied Biosystems). Before conducting population and landscape genetics analyses, we examined HW and linkage equilibrium in our microsatellite data using option 1 and 2 of the web version of GENEPOP 4.0.10 (Raymond & Rousset 1995). Sample sites with ≥ 20 individuals were used for these analyses (10 sites, Supporting material 6.8.1). We assessed disequilibrium after sequentially adjusting *P*-values for multiple tests in each sample site (Hochberg 1988).

6.3.5 Genetic structure

To determine if fire mosaics affected gene flow in *N. stellatus*, we analysed our microsatellite data with two different Bayesian clustering methods. Both methods use a Markov-chain Monte Carlo (MCMC) algorithm to identify the most likely number of genetic clusters (*K*) in the data at Hardy-Weinberg equilibrium, then assign individuals probabilistically to a cluster (Pritchard et al. 2000). Thus, effects of fire mosaics on gene flow could be identified if spatial fire boundaries corresponded to genetic clusters. We conducted the analyses separately for each reserve, and then on the overall sample. First, we used a non-spatial model implemented in STRUCTURE 2.3.2 (Pritchard et al. 2000). Second, we used a spatial model implemented in GENELAND 3.3.0 which is similar to STRUCTURE, but includes geographic coordinates for each individual (Guillot et al. 2005). This makes GENELAND more sensitive to weak genetic structure because spatially clustered individuals have a higher probability of being in the same genetic cluster (Guillot et al. 2005).

We ran STRUCTURE using the admixture and correlated allele frequency models for 500,000 MCMC repetitions after a burn-in of 200,000. Five independent runs of each *K* from 1 to 8 were conducted. We inferred the number of clusters in each data set by selecting the *K* with the highest mean estimated model log-likelihood ($\ln\Pr(X|K)$) across the independent runs (Pritchard et al. 2000). We ran GENELAND for 500,000 MCMC repetitions and allowed *K* to vary between 1 and 10. The Dirichlet allele frequency model was used because the correlated allele frequency model can overestimate *K* (Guillot et al. 2005), and we found it was unstable in preliminary analyses. We set spatial uncertainty of the coordinates at 1000 m to allow for potentially large home ranges in the lizards. We discarded the first 125,000 repetitions and then inferred *K* from the mode of the posterior distribution. Five independent runs were conducted to check for consistency of results.

6.3.6 Landscape resistance

To further analyse dispersal across fire mosaics in *N. stellatus*, we developed a set of landscape resistance models based on five features we considered to be important to gene flow: isolation by distance, elevation, time since fire, abundance, and fire frequency (Table 6.1). The fire frequency model was only tested for Hincks because it had a more complex fire history than the other three reserves (Supporting material 6.8.1). We examined the relationship between each landscape resistance model and genetic distance between individual geckos as a measure of gene flow (more detail below). We compiled the landscape models on raster grids with 20 m resolutions in ArcMap 9.2 (ESRI). To estimate resistance from each model we used a method based on circuit theory which takes into account all possible pathways between individuals (McRae & Beier 2007). Thus, to account for potentially long-distance dispersal, we defined the extent of our study landscapes with a 5 km buffer around the samples for each of the four data sets.

Table 6.1. We tested models of landscape resistance based on five features considered to be important to gene flow in *Nephrurus stellatus*. The fire frequency landscape was examined for Hincks only.

Spatial model	**Grid cell values**	**Potential ecological importance**
Isolation by distance	1	Genetic distance can increase with geographic distance (Wright 1943).
Elevation	Metres above sea level	Sand dunes are the dominant elevational features in our study system (Twidale & Campbell 1985). *N. stellatus* is more common on dunes than swales (Williams et al. 2011) probably because it is a burrower (Wilson & Swan 2010) and is associated with open ground (Smith et al. 2012). Gene flow may be influenced by elevation (representing the topography of the dunes) if dunes affect their dispersal ability.
Time since fire	Number of years since most recent fire (1- 57)	Marked changes in vegetation structure with time since fire occur at our study sites (Smith et al. 2012)and habitat structure can affect dispersal in lizards (Berry et al. 2005; Templeton et al. 2011).
Abundance	Mean no. captures predicted from time since fire (Smith et al. Chapter 3)	*N. stellatus* is not affected linearly by fire; habitat with 5-10 years since fire is most suitable (Driscoll et al. 2012a; Smith et al. 2012). Dispersal through unsuitable habitat may be inhibited (Prevedello et al. 2010; Shanahan et al. 2011) or promoted (Driscoll & Hardy 2005; Schtickzelle et al. 2007). Variation in population density can influence gene flow and dispersal (Stephens et al. 1999; Konvicka et al. 2012).
Fire frequency	Number of fires since 1953 (0-5)	Fire can have cumulative effects on animal populations (Lindenmayer et al. 2008) either through demographic impacts of repeated burning (Westgate et al. 2012), or changes in habitat structure (Pausas & Lloret 2007) that might affect gene flow.

The isolation by distance (IBD) model produced a "flat" landscape and accounted for the extent of the study area (Lee-Yaw et al. 2009). Significant positive IBD would suggest that gene flow decreases with increasing geographic distance between sample locations. The elevation model tested if gene flow was inhibited or promoted by sand dunes – the dominant topographic features in our study landscapes (Table 6.1). Positive coefficients for the elevation model would indicate lower gene flow at higher elevations. For the time since fire (TSF) model, positive coefficients would indicate that the habitat becomes more resistant to gene flow with increasing time since fire in a linear way (Table 6.1). The abundance was based on the same spatial configuration as the TSF model but parameterised with the predicted abundance for a given TSF (more detail below). The population response to TSF in *N. stellatus* is not linear, so the abundance model allowed us to examine demographic or habitat related changes in gene flow that may be related to their non-linear population response (Table 6.1). High values specified high resistance, so positive coefficients for the abundance model would suggest reduced gene flow in habitats where the animals were most common. For the fire frequency model, positive coefficients would suggest that gene flow decreases with increased number of fires in a habitat (Table 6.1).

Our elevation data were sourced from the Shuttle Radar Topographic Mission one-second bare earth version of Australia (CSIRO 2011). Elevations were projected as points from WGS84 to GDA94 (Universal Transverse Mercator zone 53), then interpolated with ANUDEM (Hutchinson 2011) to create digital elevation models for our study landscapes. The three fire-related models were derived from two different polygon layers containing the extent and year of the most recent fire (time since fire (Fig. 6.1) and abundance models) and of all fires (fire frequency model, Supporting material 6.8.1) since 1953 (South Australian Department for Environment and Natural Resources). For the abundance model we used the mean number of captures predicted from time since fire (Smith et al. Chapter 3) which enabled us to parameterise areas we had not sampled. Estimates were available for Hincks and Pinkawillinie only so we used values from Hincks for Munyaroo and Heggaton, as these sites were most similar genetically (see 6.4 Results) and the fire response in *N. stellatus* is regionally similar (Driscoll & Henderson 2008).

For each landscape model we calculated the resistance between all pairs of individuals within each reserve using CIRCUITSCAPE 3.5.4 (McRae & Beier 2007). We used

SPAGEDI 1.2 (Hardy & Vekemans 2002) to calculate genetic distance between all pairs of individuals as a_r, an individual analogue to $F_{ST} / (1 - F_{ST})$ (Rousset 2000). We used regression of distance matrices (Legendre et al. 1994) to examine the relationship between genetic distance and landscape resistance for each spatial model separately. The MRM function in ecodist (Goslee & Urban 2007) for R 2.14 (R Development Core Team 2011) was used to fit the models, and *P*-values were generated with 10,000 simultaneous permutations of the rows and columns of the dependent variable matrix (Legendre et al. 1994). Our spatial fire data were restricted to the reserves but the buffers extended outside these areas. Thus, for each of the three fire-related models, we initially tested if the agricultural land outside the reserves had either high or low resistance to gene flow. Two different parameterisations for the agricultural land were tested using the minimum and maximum values from each landscape model. The model with the highest R^2 was then used in the main analysis.

6.3.7 Genetic diversity

Restricted dispersal can cause declines in genetic diversity, so we analysed variation in genetic diversity across fire mosaics in *N. stellatus*. We examined the effect of time since fire on two measures of genetic diversity: site-level allelic richness (AR) and individual heterozygosity. We used standArich (Alberto 2006) in R to calculate AR standardised for sample size (N). It was only possible to examine effects of time since fire on AR when N was small because sites in the long-unburnt habitat always had small sample sizes. We thus calculated AR for N = 5 to include a wide range of times since fire. For comparison with larger sample sizes, we also calculated AR for N = 6 to 10, however as N increased, the number of sites with long times since fire decreased. For each N, we calculated the mean AR from 100 random samples from each site (Leberg 2002). We used linear mixed models in lme4 (Bates et al. 2011) to examine the effect of time since fire (TSF) on AR for each N. Because we sampled multiple sites within a single fire boundary we fitted fire (a factor naming individual fire events) as a random effect. TSF and reserve were fitted as fixed effects and our starting model included their main and interactive terms. To estimate the effect of TSF on individual genetic diversity we first calculated the proportion of typed loci that were heterozygous in each individual. We modelled heterozygosity with the same formulation as for AR, but also included site as an additional random term to account for potential dependence among individuals in the same site.

For both the allelic richness and heterozygosity analyses, we calculated *P*-values using Wald tests (Welsh 1996). If the interactive term was not significant ($P > 0.05$) we removed it, and subsequently removed reserve if it was not significant in the resulting model (Zuur et al. 2009). Parameter estimates and standard errors were obtained using the AICcmodavg package (Mazerolle 2011).

6.3.8 Movement rates

To determine if post-fire succession affected direct measures of movement in *N. stellatus*, we analysed mark-recapture data from the grid sites (Hincks and Pinkawillinie only, Supporting material 6.8.1). For all animals that were captured more than once, we calculated the distance moved and number of days between capture and subsequent capture. If an animal was captured more than twice, each movement event was included as a separate observation (e.g. an animal captured four times had three movement observations). A single movement will almost certainly under estimate the actual distance moved between the two captures. Furthermore, our observations were restricted to the 1 ha scale of the trapping grids, with the longest movement recorded at 120 m. Longer movement events will therefore be under-represented in the data.

We restricted our analyses to the recaptures that occurred within a single trapping period (≤ 15 days) because only five recaptures were recorded between trapping periods at the long-unburnt sites making rigorous comparisons of different post-fire habitats over longer trapping periods impossible. Capture rates in *N. stellatus* are strongly dependent on temperature (Smith et al. 2012), and our preliminary analysis showed that minimum temperature between captures had greater explanatory power than the mean or maximum temperature (geckos moved shorter distances when minimum temperatures were lower). All of our models of movement rates therefore included minimum temperature as a numeric predictor. Because there was a high proportion of zeros in our data (30 %) we first investigated if time since fire (TSF) affected the propensity of geckos to move or not to move between captures. We fitted TSF and minimum temperature (both numeric predictors) as fixed effects in a generalised linear mixed model with a binomial distribution and logit link function in lme4 (Bates et al. 2011). Thirty-two percent of geckos were measured more than once so we included individual as a random effect. To account for our grouped sampling design (2 grids were sampled within a single fire boundary) we also fitted fire as a random effect.

We then considered the effect of TSF on movement rates (metres moved / number of days between captures) only for geckos that moved. We used the log (movement rate) because it gave the best approximation to a normal distribution. We developed a set of 12 candidate models to examine effects of TSF and minimum temperature (included in all models) and three covariates: sex, age and reserve. The candidate set included the global model (all covariates) and all additive formulations nested within it. We also included first order interactions of the covariates with TSF. We initially fitted individual (18 % of geckos were measured more than once) and fire as random effects in linear mixed models. However, the variance on both random terms was approximately zero so we removed them to reduce the number of parameters. The final models were fit using linear regression in R and ranked by AICc weight (Burnham & Anderson 2002). We used model averaging to obtain parameter estimates and standard errors with AICcmodavg (Mazerolle 2011). We inferred significance of the terms from the effect sizes of the model averaged estimates and confidence intervals.

6.4 Results

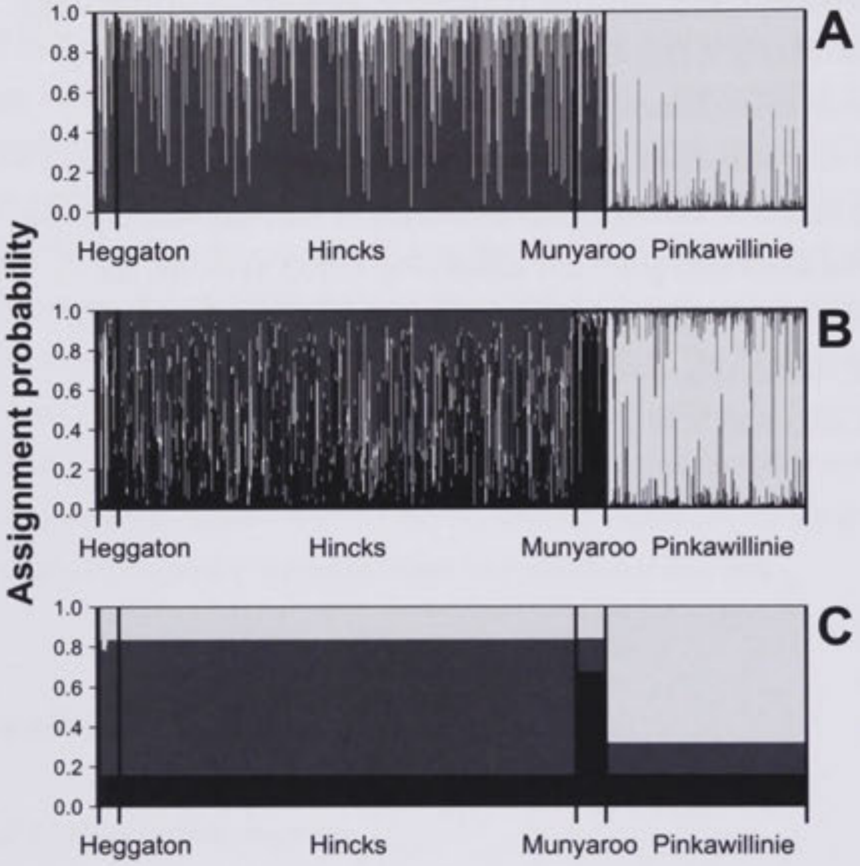
6.4.1 Genetic data properties

Our microsatellite data set included genotypes for 764 *Nephrurus stellatus* individuals at 14 loci (Supporting material 6.8.1). Of the ten sample sites where $N \geq 20$, only one locus at one site showed evidence of HW disequilibrium (NeSt28 at HIM2). Of 862 pairs of loci examined, there was evidence of linkage disequilibrium in a single locus pair at six different sites: HIE1 (NeSt38 and NeSt35), HIE2 (NeSt47 and NeSt35), HIM1 (NeSt23 and NeSt33), PE2 (NeSt09 and NeSt28), PM1 (NeSt23 and NeSt28), and PM2 (NeSt18 and NeSt33). Given that there were no consistent patterns of disequilibrium we considered all loci were in HW and linkage equilibrium.

6.4.2 Genetic structure

We identified a single genetic cluster (*K*) within each reserve using both STRUCTURE and GENELAND (Supporting material 6.8.2) indicating high gene flow within reserves. In the combined analysis of samples from all reserves, $K = 3$ had the highest probability using both methods (Supporting material 6.8.2). However, we presented STRUCTURE results from $K = 2$ and 3 (Fig. 6.2) as these had similar probabilities and the smaller estimate is more conservative (Pritchard et al. 2007). When $K = 2$ there was differentiation between Pinkawillinie and the other three reserves (Fig. 6.2a). When $K = 3$ Pinkawillinie and Munyaroo showed genetic differentiation from each other and from Hincks and Heggaton which were genetically similar (Fig. 6.2b,c). However, the genetic differentiation was not strong as STRUCTURE assigned individuals within reserves to different clusters (Fig. 6.2a,b) and assignment probabilities from GENELAND were never > 68 % (Fig. 6.2c).

Fig. 6.2 Probabilities of assignment to genetic clusters for *Nephrurus stellatus* genotypes (each bar represents an individual gecko). In the overall sample, STRUCTURE identified (A) two or (B) three clusters and (C) GENELAND identified three.



6.4.3 Landscape resistance

At Hincks, the time since fire (TSF) and fire frequency landscape models explained significant variation in genetic distance between pairs of individual geckos (Table 6.2). Genetic distance increased with increasing TSF at Hincks, and genetic distance was lower in areas that had experienced more fires, than in areas with fewer fires (Table 6.2). At Pinkawillinie neither of the fire-related models were significant. However, there was significant isolation by distance at Pinkawillinie, showing an increase in genetic distance with increasing geographic distance, and higher elevations were related to greater genetic distance between individuals (Table 6.2). No landscape models explained significant variation in genetic distance at Munyaroo or Heggaton (Table 6.2).

Table 6.2 Results from regression of genetic and landscape distance matrices. Significant relationships ($\alpha = 0.05$) are shown in bold.

Model	Relationship	R^2	*P*-value
HINCKS			
Isolation by distance	+	0.0003	0.259
Elevation	+	0.0005	0.120
Time since fire	+	**0.0038**	**0.020**
Abundance	-	0.0019	0.061
Fire frequency	**-**	**0.0017**	**0.003**
HEGGATON			
Isolation by distance	+	0.0001	0.257
Elevation	+	0.0001	0.263
Time since fire	+	0.0002	0.265
Abundance	-	0.0001	0.402
MUNYAROO			
Isolation by distance	+	0.0015	0.393
Elevation	+	0.0011	0.464
Time since fire	-	0.0002	0.836
Abundance	+	0.0069	0.430
PINKAWILLINIE			
Isolation by distance	+	**0.0040**	**0.004**
Elevation	+	**0.0049**	**0.002**
Time since fire	+	0.0024	0.225
Abundance	+	0.0001	0.685

6.4.4 Genetic diversity

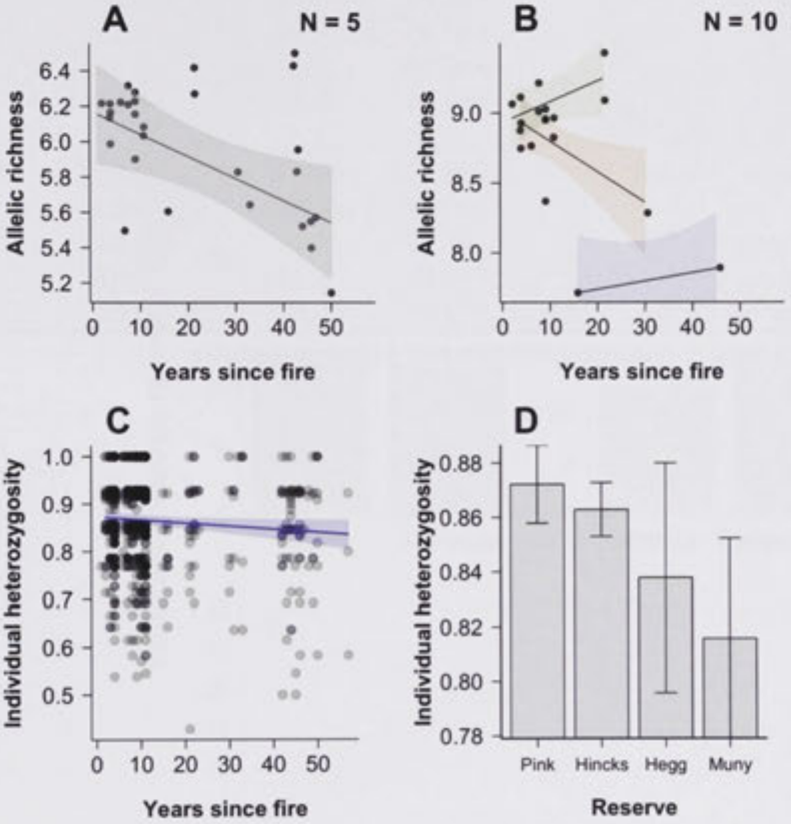
We found a significant decrease in site-level allelic richness (AR) with increasing TSF when the sample size (N) was standardised for five individuals, and there were no interactive or main effects of reserve (Table 6.3, Fig. 6.3a). When N = 6, 7, and 10 there were significant main and interactive effects of TSF and reserve on AR (Table 6.3, Fig. 6.3b). At these sample sizes, relationship between AR and TSF differed among reserves, decreasing at Hincks, increasing at Pinkawillinie and having no response at Munyaroo (Fig. 6.3b, Supporting material 6.8.3). When N = 8 and 9 there was no effect of TSF on AR but a significant effect of reserve (Table 6.3, Supporting material 6.8.3). AR was higher at Pinkawillinie than Hincks and lowest at Munyaroo (Supporting material 6.8.3). We could not include Heggaton in the models when N > 5 as there was only one site (Supporting material 6.8.3).

Table 6.3 *P*-values from linear mixed models to examine the effect of time since fire (TSF) and reserve on site-level allelic richness and individual heterozygosity in *Nephrurus stellatus*.

Response	N random subsamples	TSF	Reserve	TSF x Reserve
Allelic richness	5	0.013	-	-
	6	< 0.001	0.021	0.011
	7	< 0.001	0.006	0.007
	8	0.108	< 0.001	-
	9	0.144	< 0.001	-
	10	0.018	< 0.001	0.016
Heterozygosity	-	0.042	0.032	-

We found significant main effects of TSF and reserve on individual heterozygosity (Table 6.3, Fig. 6.3c-d). Heterozygosity decreased significantly with increasing TSF (Fig. 6.3c) and was lower at Hincks than Pinkawillinie and lowest at Munyaroo (Fig. 6.3d). The confidence interval for Heggaton was too wide for reliable inference (Fig. 6.3d). Results from both measures of genetic diversity showed generally congruent patterns of decreasing genetic diversity with increasing TSF.

Fig. 6.3 The predicted effects (± 95 % CI) of time since fire (TSF) and reserve on genetic diversity in *Nephrurus stellatus* shown over the raw data. Allelic richness was affected by (A) TSF when N = 5 and by (B) TSF x reserve when N = 10 (Pinkawillinie, Hincks and Munyaroo are shown in green, red and purple, respectively). Individual heterozygosity was affected by (C) fire and (D) reserve.



6.4.5 Movement rates

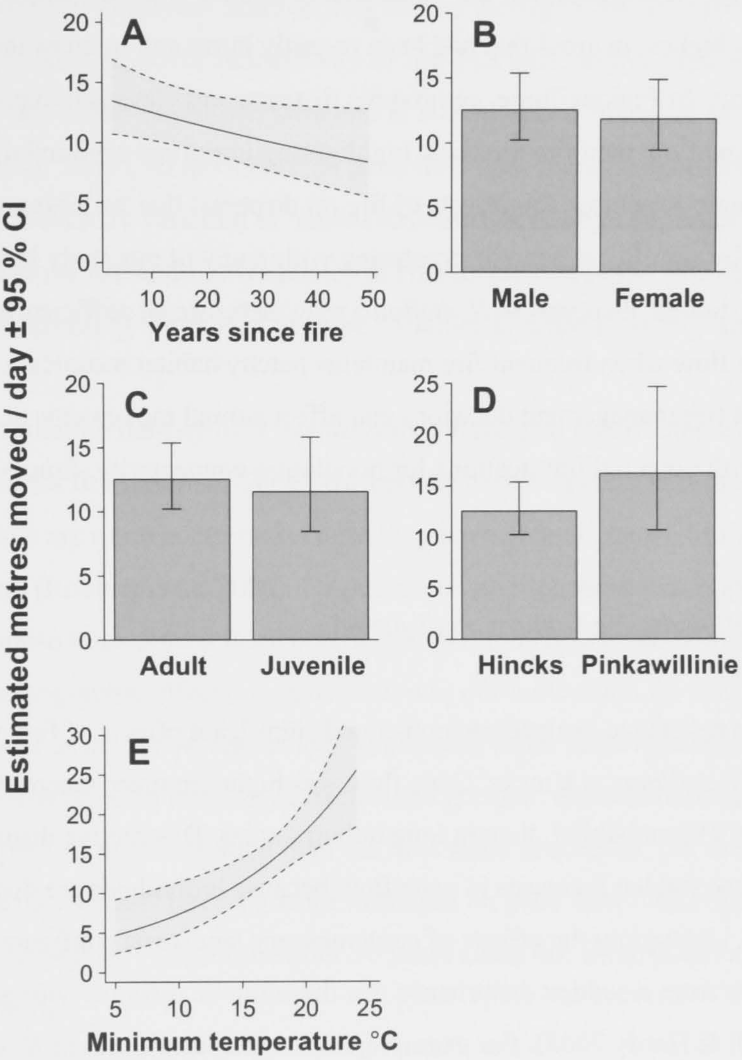
All 12 models of *N. stellatus* movement rates in our candidate set were similar (Delta AICc ≤ 5.5, Table 6.4). Model averaged parameter estimates (Fig. 6.4) showed a significant decline in movement rate with increasing TSF (Fig. 6.4a). There was an increase in the distance moved per day with increasing minimum temperature (Fig. 6.4e). Effects of sex, age and reserve were not significant (Fig. 6.4b-d).

Table 6.4. Candidate models to examine variables affecting the distance moved per day in *Nephrurus stellatus* individuals.

Predictor variables	No. parameters	AICc	Delta AICc	AICc weight
TSF + temp + reserve	5	186.50	0.00	0.23
TSF + temp + age + reserve	6	186.87	0.37	0.19
TSF + temp + TSF x sex	6	187.23	0.73	0.16
TSF + temp + sex + reserve	7	188.10	1.59	0.10
TSF + temp + TSF x age	5	188.20	1.70	0.10
TSF + temp + age	5	189.50	3.00	0.05
TSF + temp + sex + age + reserve	8	190.04	3.54	0.04
TSF + temp	4	190.15	3.65	0.04
TSF + temp + sex	6	190.38	3.88	0.03
TSF + temp + TSF x temp	5	191.55	5.04	0.02
TSF + temp + TSF x reserve	5	191.87	5.37	0.02
TSF + temp + sex + age	7	192.00	5.50	0.01

TSF = time since fire, temp = minimum temperature between captures

Fig. 6.4. Model averaged movement rates in *Nephrurus stellatus*. Estimates of each term in the candidate model set are shown: (A) time since fire, (B) sex, (C) age, (D) reserve, and (E) minimum temperature.



6.5 Discussion

Our study was one of the first to combine genetic and direct methods to study animal dispersal across fire mosaics (see also Templeton et al. 2001; Templeton et al. 2011). The fire specialist gecko *Nephrurus stellatus* experiences a marked decline in population density beyond approximately ten years since fire, and we asked whether this response was accompanied by changes in dispersal. Our direct estimates of movement, analysis of genetic diversity, and our analysis of landscape resistance at

Hincks provided evidence that dispersal declined with increasing time since fire. Geckos in late successional habitats moved shorter distances per day and had the lowest levels of allelic richness and heterozygosity. Our largest DNA sample size came from Hincks which also had the widest range of times since fire and the most complex history of repeated fires. At this location, our landscape resistance analysis demonstrated that gene flow was highest in areas that had been recently burnt and in areas that had been frequently burnt. At Pinkawillinie, geographic distance and elevation explained more variation in gene flow than fire mosaics, highlighting important regional differences in landscape genetic structure. The effects of fire on dispersal that we observed were not accompanied by significant genetic structuring within any of our study landscapes. At the scales we studied, dispersal in *N. stellatus* may therefore be sufficiently high to maintain gene flow when frequent fire maintains patchy habitat mosaics. Our study highlights that fire management decisions can affect animal movements across landscapes, with potential implications for population connectivity, fitness and adaptive potential.

6.5.1 Effects of landscape features on dispersal

Our landscape resistance analyses demonstrated significant effects of fire mosaics on gene flow in *N. stellatus* at Hincks. Gene flow was higher in more recently burnt, and more frequently burnt habitat, than in long unburnt areas. Destructive disturbances such as fire can cause sudden increases in gene flow because individuals are displaced (Porter 1999). Untangling the effects of contemporary landscape configuration with residual effects from a sudden disturbance can therefore be difficult with genetic data alone (Driscoll & Hardy 2005). For example, current dispersal rates in *N. stellatus* could be equal in all post-fire stages, but a signal of increased gene flow in recently burnt sites could arise from an initial influx of individuals immediately after fire. In our study however, direct observations of movement declined continually with increasing time since fire, indicating a current and ongoing effect of habitat succession on dispersal. Our study therefore provides strong evidence that fire mosaics can affect dispersal in *N. stellatus*.

The effects of fire mosaics on gene flow at Hincks could relate either to variation in habitat structure, demographic processes, or a combination of these factors. Habitat structure at our sites is strongly affected by post-fire succession (Smith et al. 2012) and this may affect the ability of geckos to move, forage and successfully disperse (Prevedello et al. 2010; Templeton et al. 2011). Our direct measures of movement support this suggestion. Adult male geckos moved an estimated 13 m per day in habitats with five years since fire, and this declined to 8 m per day at 50 years since fire. Our results therefore have important implications for fire management: the spatial scales of fire mosaics are likely to affect connectivity of fire specialist animals species. Fire frequency can also affect vegetation structure at a local scale (Pausas & Lloret 2007; Vilà-Cabrera et al. 2008), so the increased gene flow with increasing number of fires may have been driven by variation in habitat structure driven by fire frequency. However, time since fire and fire frequency at Hincks are correlated (Smith et al. Chapter 7), so separating the effects of these variables is difficult in this landscape.

Variation in population density of *N. stellatus* may have also contributed to the changes in gene flow across fire mosaics. Gene flow may be higher in early successional habitats where the geckos are more common because they have greater chance of finding mates and reproducing (Robinet et al. 2008). Dispersal can also increase with population density in response to increased interspecific competition (Bowler & Benton 2005). The potential for demographic effects on gene flow was our motivation for testing the abundance model of landscape resistance. Abundance is not linearly related to time since fire in *N. stellatus*, so if density effects were greatest, the abundance model would likely have explained more variation than the time since fire model, but this was not the case. Habitat structure may have a greater influence on gene flow than population density, but both probably contribute after 10 years since fire when population density starts to decline.

We found that both allelic richness and individual heterozygosity declined with time since fire in *N. stellatus*. Reduced genetic diversity often accompanies restricted gene flow in lizards (Berry et al. 2005; Hoehn et al. 2007; Levy et al. 2010) and our results from *N. stellatus* may reflect reduced dispersal with time since fire. The reduction in population density with advanced succession could have contributed to the reduced genetic diversity (Frankham 1996). In an informative contrast to our work, Schrey et al. (2011) studied a late-successional lizard and found that microsatellite genetic diversity increased with time since fire. Genetic diversity measured from microsatellites is often correlated with adaptive diversity and population declines can cause greater reduction in adaptive than neutral genetic diversity (Sutton et al. 2011). Species living with unfavourable fire regimes may therefore have a reduced ability to adapt to changing environmental and demographic conditions (Templeton et al. 2001; Keller & Waller 2002).

At Pinkawillinie elevation and geographic distance, rather than the post-fire landscape, explained significant genetic distance among individuals. Higher elevations, which represented the sand dunes in our study landscapes, were associated with lower gene flow at Pinkawillinie. Williams et al. (2011) recorded *N. stellatus* more commonly on dunes than in swales. However, the abundance model at Pinkawillinie was not significant, so the effect of elevation may related to the habitat rather than its effect on population density. *Nephrurus stellatus* dig burrows, so they may have a tendency to remain in sandy areas where they can burrow and avoid the swales between the dunes. We did not find effects of elevation on gene flow at Hincks, but the dune system differs between Hincks and Pinkawillinie. The topography at Pinkawillinie consists predominantly of a large, irregular, parabolic dune field, while Hincks has regularly undulating longitudinal dunes. The irregularity of the dune system at Pinkawillinie may create large areas unsuitable for movement which may not be evident at Hincks if the dispersal distance is greater than the distance between dunes.

The effect of fire on gene flow at Hincks but not Pinkawillinie could be related to differences in the spatial configuration of fire mosaics. At Hincks, a recent fire separates the long unburnt mallee from the mid-successional habitat. At Pinkawillinie, the samples were collected along a gradient from recently burnt to long unburnt habitat. Our results highlight the importance of examining barriers to dispersal across multiple landscapes to understand regional variation in gene flow (Short Bull et al. 2011). We did not find effects of landscape features on gene flow in *N. stellatus* at Munyaroo or Heggaton but this may have been because of the smaller sample sizes in these reserves.

6.5.2 Genetic structure in Nephrurus stellatus

The lack of genetic structure within reserves suggests that gene flow in *N. stellatus* remains high despite the effects of fire mosaics and topography on dispersal that we observed. Significant microsatellite genetic structure has been detected in several lizard species at similar spatial scales to those we studied (< 20 km) using genetic cluster analyses (Stow et al. 2001; Berry et al. 2005; Smith et al. 2009; Dubey & Shine 2010;

Levy et al. 2010). Most of the species studied previously were habitat specialists. For example, lizards that inhabit rocky outcrops within grasslands had strong genetic structure related to their patchy habitat (Stow et al. 2001; Berry et al. 2005; Levy et al. 2010). In temporally stable habitats, theory predicts that low dispersal rates will evolve with habitat specialisation (Kisdi 2002). However, in regularly disturbed habitats high dispersal should evolve to allow movement among continually changing habitat patches (Travis & Dytham 1999). Species that colonise disturbed habitats rapidly are predicted to have the highest dispersal rates (Connell & Slatyer 1977) and studies of invertebrate communities have demonstrated this empirically (Steffan-Dewenter & Tscharntke 1997; Entling et al. 2011; Langlands et al. 2011). Thus, *N. stellatus* may have higher dispersal rates than lizard species in more stable environments so they can disperse through their temporally dynamic habitat and colonise areas quickly following fire.

Three possible mechanisms could promote the high gene flow within reserves that we observed in *N. stellatus*. First, long distance dispersal, even at low rates, can eliminate genetic structure (Mills & Allendorf 1996) which could allow *N. stellatus* to maintain connectivity across fire mosaics. Hoehn et al. (2007) suggested that the wide-spread, generalist gecko *Gehyra variegata* persisted in a highly modified agricultural system because of long-distance dispersal (> 1 km). Second, maintenance of low-density populations in long-unburnt habitat may facilitate gene flow. We often captured *N. stellatus* in low numbers outside their preferred habitat (> 30 years since fire) and previous studies suggested they can remain resident in these areas for at least two years (Smith et al. 2012). Long-unburnt mallee may serve as either a permanent but sub-optimal habitat for *N. stellatus*, a permeable matrix, or both. A third explanation for the lack of genetic structure within reserves is that the temporal scale of fires in relation to generation time may have been insufficient to detect any effects (Landguth et al. 2010). Mallee can remain unburnt for well over a century (Clarke et al. 2010) so it will be important in future studies to determine if early successional species can persist in landscapes where fire has been absent for longer time scales that we examined in this study.

We found that gene flow in *N. stellatus* was restricted among reserves separated by over 100 km of mostly agricultural land. However, the spatial overlap in genetic clustering suggested that, even at this scale, gene flow has not been strongly restricted. This study focussed on dispersal within reserves, so we cannot currently determine if this reflects ongoing dispersal through the agricultural matrix, or a residual signal of gene flow from previously connected habitats. However, analysis of *N. stellatus* patch occupancy suggests that dispersal may be highly restricted in agricultural landscapes (Driscoll et al. 2012b).

6.5.3 Conclusions & future directions

Our study has made substantial progress in determining how animal dispersal varies among habitat patches that differ predominantly in their successional development after fire. We found evidence that movement, gene flow and genetic diversity in *N. stellatus* declined with increasing time since fire, suggesting that the strong decline in population density with advanced habitat succession is accompanied by declines in dispersal. Complex vegetation structure may inhibit movement in long unburnt habitats, and geckos may have a reduced chance of finding mates, leading to lower gene flow and genetic diversity. Our findings highlight that fire management decisions have the potential to affect connectivity and adaptive potential of animal populations in fire prone ecosystems.

Our findings raise important questions for future research. First, a wide range of species need to be considered in fire management planning, so the effects of fire regimes on dispersal in other animal taxa need to be quantified. Many mallee bird (Bradstock et al. 2005; Brown et al. 2009), mammal (Friend 1993; Kelly et al. 2011), and invertebrate species (Teasdale et al. in review) show strong distributional responses to post-fire succession, and the consequences of these effects on their dispersal is largely unknown. Second, our study targeted areas of mallee that had complex fire mosaics, but the effects of widespread burning, or long-term fire suppression on dispersal remain unknown. We found that gene flow in *N. stellatus* was influenced by post-fire succession, and it is possible that more extreme fire regimes could substantially restrict gene flow in this and other species. Third, we examined fire mosaics only in large, continuous conservation reserves. However, over 60 % of the native vegetation on the Eyre Peninsula has been cleared for agriculture and ecosystems around the world face similar problems. It is therefore critical that the interactive effects of fire and fragmentation on animal dispersal are given attention in future (Driscoll et al. 2010).

Temporally dynamic habitats may promote high dispersal rates in animals so they can recolonise habitats when they become suitable following disturbance. However, in many areas of the world natural fire regimes have been strongly disrupted and management agencies are often challenged with making decisions that will affect biodiversity. Fire suppression has caused declines in species relying on early successional habitats in many regions (e.g. Betts et al. 2010), while animal declines have accompanied recent increases in fire frequency and intensity in other regions (e.g. Woinarski et al. 2011). We have shown that fire mosaics can influence dispersal in a fire specialist species. Thus fire management must be conducted at spatial and temporal scales that allow animal species to maintain connectivity across landscapes. Restricted dispersal may be one mechanism driving declines in species living with inappropriate fire regimes. Incorporating information about animal dispersal into fire management plans is likely to increase the chance of conserving biodiversity.

6.6 Acknowledgements

Over 100 volunteers were involved in collecting samples for this project, and substantial field assistance was provided by Samantha Blight, Simone Dalgairns, Juliana Lazzari, Kevin Mayes, Andrew Murphy, Sally South, and Catherine Whitehead. Many thanks to Kathy Saint, Terry Bertozzi, and Steve Donnellan at the South Australian Museum for assistance with molecular data collection. The South Australian Department of Environment and Natural Resources (SA DENR), particularly Joe Tilley from the Pt Lincoln branch, provided logistical support in the field. John Stein kindly created digital elevation models and gave advice on spatial data analysis. This research was supported by funds from the Australian Research Council, the Wildlife Conservation Fund, The Australian National University, The Sir Mark Mitchell Research Foundation, The Lirabenda Endowment Fund, and the Ecological Society of Australia. We worked under scientific permit S25589 (SA DENR) and animal ethics permit E256 (Flinders University).

6.7 References

Alberto F. (2006). *standArich: an R package to estimate population allelic richness using standardized sample size.* CCMAR, University of the Algarve, Portugal. http://www.ccmar.ualg.pt/maree/software.php?soft=sarich.

Banks S.C., Blyton M.D.J., Blair D., McBurney L. and Lindenmayer D.B. (2012). Adaptive responses and disruptive effects: how major wildfire influences kinship-based social interactions in a forest marsupial. *Molecular Ecology* 21: 673-684.

Banks S.C., Dujardin M., McBurney L., Blair D., Barker M. and Lindenmayer D.B. (2011). Starting points for small mammal population recovery after wildfire: recolonisation or residual populations? *Oikos* 120: 26-37.

Banks S.C., Lindenmayer D.B., Ward S.J. and Taylor A.C. (2005). The effects of habitat fragmentation via forestry plantation establishment on spatial genotypic structure in the small marsupial carnivore, *Antechinus agilis*. *Molecular Ecology* 14: 1667-1680.

Bates A.J., Sadler J.P. and Fowles A.P. (2006). Condition-dependent dispersal of a patchily distributed riparian ground beetle in response to disturbance. *Oecologia* 150: 50-60.

Bates D., Maechler M. and Bolker B. (2011). *lme4: linear mixed-effects models using S4 classes.* R package, version 0.999375-40. http://lme4.r-forge.r-project.org/ (accessed September 2011).

Berry O., Tocher M.D., Gleeson D.M. and Sarre S.D. (2005). Effect of vegetation matrix on animal dispersal: genetic evidence from a study of endangered skinks. *Conservation Biology* 19: 855-864.

Betts M.G., Hagar J.C., Rivers J.W., Alexander J.D., McGarigal K. and McComb B.C. (2010). Thresholds in forest bird occurrence as a function of the amount of early-seral broadleaf forest at landscape scales. *Ecological Applications* 20: 2116-2130.

Bowler D.E. and Benton T.G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews* 80: 205-225.

Bradstock R.A., Bedward M., Gill A.M. and Cohn J.S. (2005). Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. *Wildlife Research* 32: 409-423.

Bradstock R.A. and Cohn J.S. (2002). Fire regimes and biodiversity in semi-arid mallee ecosystems. In: *Flammable Australia: the fire regimes and biodiversity of a continent.* (eds. Bradstock RA, Williams JE, Gill AM). Cambridge University Press, Cambridge.

Broquet T. and Petit E.J. (2009). Molecular estimation of dispersal for ecology and population genetics. *Annual Review of Ecology, Evolution and Systematics* 40: 193-216.

Brotons L., Pons P. and Herrando S. (2005). Colonization of dynamic Mediterranean landscapes: where do birds come from after fire? *Journal of Biogeography* 32: 789-798.

Brown S., Clarke M. and Clarke R. (2009). Fire is a key element in the landscape-scale habitat requirements and global population status of a threatened bird: the mallee emu-wren (*Stipiturus mallee*). *Biological Conservation* 142: 432-445.

Burnham K.P. and Anderson D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer-Verlag, New York.

Clarke M.F. (2008). Catering for the needs of fauna in fire management: science or just wishful thinking? *Wildlife Research* 35: 385-394.

Clarke M.F., Avitabile S.C., Brown L., Callister K.E., Haslem A., Holland G.J., Kelly L.T., Kenny S.A., Nimmo D.G., Spence-Bailey L.M., Taylor R.S., Watson S.J. and Bennett A.F. (2010). Ageing mallee eucalypt vegetation after fire: insights for successional trajectories in semi-arid mallee ecosystems. *Australian Journal of Botany* 58: 363-372.

Cogger H.G. (1996). *Reptiles and amphibians of Australia.* Reed, Port Melbourne, VIC.

Connell J.H. and Slatyer R.O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist* 111: 1119-1144.

CSIRO (2011). *One-second SRTM digital elevation model.* Commonwealth Scientific and Industrial Research Organisation. http://www.csiro.au/science/One-second-SRTM-Digital-Elevation-Model.html.

Cushman S.A. and Lewis J.S. (2010). Movement behavior explains genetic differentiation in American black bears. *Landscape Ecology* 25: 1613-1625.

Cushman S.A., McKelvey K.S., Flather C.H. and McGarigal K. (2008). Do forest community types provide a sufficient basis to evaluate biological diversity? *Frontiers in Ecology and the Environment* 6: 13-17.

Cushman S.A., McKelvey K.S., Hayden J. and Schwartz M.K. (2006). Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. *The American Naturalist* 168: 486-499.

do Rosário I.T. and da Luz Mathias M. (2007). Post-fire recolonisation of a montado area by the endangered Cabrera vole (*Microtus cabrerae*). *International Journal of Wildland Fire* 16: 450-457.

Driscoll D.A. and Hardy C.M. (2005). Dispersal and phylogeography of the agamid lizard *Amphibolurus nobbi* in fragmented and continuous habitat. *Molecular Ecology* 14: 1613-1629.

Driscoll D.A. and Henderson M.K. (2008). How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model. *Biological Conservation* 141: 460-471.

Driscoll D.A., Lindenmayer D.B., Bennett A.F., Bode M., Bradstock R.A., Cary G.J., Clarke M.F., Dexter N., Fensham R., Friend G., Gill A.M., James S., Kay G., Keith D.A., MacGregor C., Russell-Smith J., Salt D., Watson J.E.M., Williams R.J. and York A. (2010). Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation* 143: 1928-1939.

Driscoll D.A., Smith A.L., Blight S.R. and Maindonald J. (2012a). Reptile responses to fire and the risk of post-disturbance sampling bias. *Biodiversity and Conservation*: DOI 10.1007/s10531-10012-10267-10535.

Driscoll D.A., Whitehead C.A. and Lazzari J. (2012b). Spatial dynamics of the knob-tailed gecko *Nephrurus stellatus* in a fragmented agricultural landscape. *Landscape Ecology*: DOI 10.1007/s10980-10012-19734-10983

Dubey S. and Shine R. (2010). Restricted dispersal and genetic diversity in populations of an endangered montane lizard (*Eulamprus leuraensis*, Scincidae). *Molecular Ecology* 19: 886-897.

Frankham R. (1996). Relationship of genetic variation to population size in wildlife. *Conservation Biology* 10: 1500-1508.

Frankham R. (1997). Do island populations have less genetic variation than mainland populations? *Heredity* 78: 311-327.

Friend G.R. (1993). Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: a review. *Biological Conservation* 65: 99-114.

Funk W.C., Donnelly M.A. and Lips K.R. (2005). Alternative views of amphibian toe-clipping. *Nature* 433: 193.

Goslee S.C. and Urban D.L. (2007). The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software* 22: 1-19.

Griffiths A.D. and Christian K.A. (1996). The effects of fire on the frillneck lizard (*Chlamydosaurus kingii*) in northern Australia. *Australian Journal of Ecology* 21: 386-398.

Guillot G., Estoup A., Mortier F. and Cosson J.-F. (2005). A spatial statistical model for landscape genetics. *Genetics* 170: 1261-1280.

Hanski I. (1998). Metapopulation dynamics. *Nature* 396: 41-49.

Hardy O.J. and Vekemans X. (2002). SPAGEDI: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Molecular Ecology Notes* 2: 618-620.

Hochberg Y. (1988). A sharper Bonferroni procedure for multiple tests of significance. *Biometrika* 75: 800-802.

Hoehn M., Sarre S. and Henle K. (2007). The tales of two geckos: does dispersal prevent extinction in recently fragmented populations? *Molecular Ecology* 16: 3299-3312.

Hutchinson M.F. (2011). *ANUDEM Version 5.3* Fenner School of Environment and Society, ANU. http://fennerschool.anu.edu.au/research/publications/software-datasets/anudem.

Keller L.F. and Waller D.M. (2002). Inbreeding effects in wild populations. *Trends in Ecology and Evolution* 17: 230-241.

Kelly L.T., Nimmo D.G., Spence-Bailey L.M., Haslem A., Watson S.J., Clarke M.F. and Bennett A.F. (2011). Influence of fire history on small mammal distributions: insights from a 100-year post-fire chronosequence. *Diversity and Distributions* 17: 462-473.

Kisdi É. (2002). Dispersal: risk spreading versus local adaptation. *The American Naturalist* 159: 579-596.

Knight T.M. and Holt R.D. (2005). Fire generates spatial gradients in herbivory: an example from a Florida sandhill ecosystem. *Ecology* 86: 587-593.

Konvicka M., Zimmermann K., Klimova M., Hula V. and Fric Z. (2012). Inverse link between density and dispersal distance in butterflies: field evidence from six co-occurring species. *Population Ecology* 54: 91-101.

Landguth E.L., Cushman S.A., Schwartz M.K., McKelvey K.S., Murphy M. and Luikart G. (2010). Quantifying the lag time to detect barriers in landscape genetics. *Molecular Ecology* 19: 4179-4191.

Lange R., Diekötter T., Schiffmann L.A., Wolters V. and Durka W. (2012). Matrix quality and habitat configuration interactively determine functional connectivity in a widespread bush cricket at a small spatial scale. *Landscape Ecology* 27: 381-392.

Leberg P.L. (2002). Estimating allelic richness: effects of sample size and bottlenecks. *Molecular Ecology* 11: 2445-2449.

Lee-Yaw J.A., Davidson A., McRae B.H. and Green D.M. (2009). Do landscape processes predict phylogeographic patterns in the wood frog? *Molecular Ecology* 18: 1863-1874.

Legendre P., Lapointe F.-J. and Casgrain P. (1994). Modeling brain evolution from behavior: a permutational regression approach. *Evolution* 48: 1487-1499.

Leidner A.K. and Haddad N.M. (2011). Combining measures of dispersal to identify conservation strategies in fragmented landscapes. *Conservation Biology* 25: 1022-1031.

Levy E., Kennington W.J., Tomkins J.L. and LeBas N.R. (2010). Land clearing reduces gene flow in the granite outcrop-dwelling lizard, *Ctenophorus ornatus*. *Molecular Ecology* 19: 4192-4203.

Lindenmayer D.B., Wood J.T., MacGregor C., Michael D.R., Cunningham R.B., Crane M., Montague-Drake R., Brown D., Muntz R. and Driscoll D.A. (2008). How predictable are reptile responses to wildfire? *Oikos* 117: 1086-1097.

Mazerolle M.J. (2011). *AICcmodavg.* R package, version 1.2. http://cran.r-project.org/web/packages/AICcmodavg/index.html (accessed September 2011).

McRae B.H. and Beier P. (2007). Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Science USA* 104: 19885-19890.

Mills L.S. and Allendorf F.W. (1996). The one-migrant-per-generation rule in conservation and management. *Conservation Biology* 10: 1509-1518.

Moretti M., de Bello F., Roberts S.P.M. and Potts S.G. (2009). Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. *Journal of Animal Ecology* 78: 98-108.

Murphy M.A., Evans J.S. and Storfer A. (2010a). Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. *Ecology* 91: 252-261.

Murphy S.A., Legge S.M., Heathcote J. and Mulder E. (2010b). The effects of early and late-season fires on mortality, dispersal, physiology and breeding of red-backed fairy-wrens (*Malurus melanocephalus*). *Wildlife Research* 37: 145-155.

Parr C.L. and Andersen A.N. (2006). Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Conservation Biology* 20: 1610-1619.

Pausas J.G. and Lloret F. (2007). Spatial and temporal patterns of plant functional types under simulated fire regimes. *International Journal of Wildland Fire* 16: 484-492.

Piggott M.P., Banks S.C. and Taylor A.C. (2006). Population structure of brush-tailed rock-wallaby (*Petrogale penicillata*) colonies inferred from analysis of faecal DNA. *Molecular Ecology* 15: 93-105.

Porter A.H. (1999). Refugees from lost habitat and reorganization of genetic population structure. *Conservation Biology* 13: 850-859.

Prevedello J.A., Forero-Medina G. and Vieira M.V. (2010). Movement behaviour within and beyond perceptual ranges in three small mammals: effects of matrix type and body mass. *Journal of Animal Ecology* 79: 1315-1323.

Pritchard J.K., Stephens M. and Donnelly P. (2000). Inference of population structure using multilocus genotype data. *Genetics* 155: 945-959.

Pritchard J.K., Wen X. and Falush D. (2007). *Documentation for structure software: version 2.2.* http://pritch.bsd.uchicago.edu/structure.html.

R Development Core Team (2011). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Raymond M. and Rousset F. (1995). GENEPOP (Version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity* 86: 248-249.

Robinet C., Lance D.R., Thorpe K.W., Onufrieva K.S., Tobin P.C. and Liebhold A.M. (2008). Dispersion in time and space affect mating success and Allee effects in invading gypsy moth populations. *Journal of Animal Ecology* 77: 966-973.

Robinson A.C. and Heard M.B. (1985). National Parks. In: *Natural history of Eyre Peninsula.* (eds. Twidale CR, Tyler MJ, Davies M). Royal Society of South Australia, Adelaide, SA.

Rousset F. (2000). Genetic differentiation between individuals. *Journal of Evolutionary Biology* 13: 58-62.

Saccheri I., Kuussaari M., Kankare M., Vikman P., Fortelius W. and Hanski I. (1998). Inbreeding and extinction in a butterfly metapopulation. *Nature* 392: 491-494.

Schooley R. and Wiens J.A. (2004). Movements of cactus bugs: patch transfers, matrix resistance, and edge permeability. *Landscape Ecology* 19: 801-810.

Schrey A.W., Fox A.M., Mushinsky H.R. and McCoy E.D. (2011). Fire increases variance in genetic characteristics of Florida Sand Skink (*Plestiodon reynoldsi*) local populations. *Molecular Ecology* 20: 56-66.

Schtickzelle N., Joiris A., Van Dyck H. and Baguette M. (2007). Quantitative analysis of changes in movement behaviour within and outside habitat in a specialist butterfly. *BMC Evolutionary Biology* 7: 4.

Schtickzelle N., Mennechez G. and Baguette M. (2006). Dispersal depression with habitat fragmentation in the bog fritillary butterfly. *Ecology* 87: 1057-1065.

Shanahan D.F., Possingham H.P. and Riginos C. (2011). Models based on individual level movement predict spatial patterns of genetic relatedness for two Australian forest birds. *Landscape Ecology* 26: 137-148.

Short Bull R.A., Cushman S.A., Mace R., Chilton T., Kendall K.C., Landguth E.L., Schwartz M.K., McKelvey K., Allendorf F.W. and Luikart G. (2011). Why replication is important in landscape genetics: American black bear in the Rocky Mountains. *Molecular Ecology* 20: 1092-1107.

Smith A.L., Bull C.M. and Driscoll D.A. (2012). Post-fire succession affects abundance and survival but not detectability in a knob-tailed gecko. *Biological Conservation* 145: 139-147.

Smith A.L., Bull C.M. and Driscoll D.A. (Chapter 3). A six-year study reveals previously undetected responses to fire in reptiles. In: *Reptile dispersal and demographics after fire: process-based knowledge to assist fire management for biodiversity*. Submitted PhD thesis, The Australian National University.

Smith A.L., Bull C.M., Gardner M.G. and Driscoll D.A. (Chapter 7). Spatial and temporal variation in genetic structure of lizards in landscapes with complex fire mosaics. . In: *Reptile dispersal and demographics after fire: process-based knowledge to assist fire management for biodiversity*. Submitted PhD thesis, The Australian National University.

Smith A.L., Gardner M.G., Bull C.M. and Driscoll D.A. (2011). Primers for novel microsatellite markers in "fire-specialist" lizards (*Amphibolurus norrisi, Ctenotus atlas* and *Nephrurus stellatus*) and their performance across multiple populations. *Conservation Genetics Resources* 3: 345-350.

Smith A.L., Gardner M.G., Bull C.M. and Fenner A.L. (2009). Restricted gene flow in the endangered pygmy bluetongue lizard (*Tiliqua adelaidensis*) in a fragmented agricultural landscape. *Wildlife Research* 36: 466-478.

Smith L.M. and Burgoyne L.A. (2004). Collecting, archiving and processing DNA from wildlife samples using FTA(R) databasing paper. *BMC Ecology* 4: http://www.biomedcentral.com/1472-6785/1474/1474.

Spear S.F. and Storfer A. (2010). Anthropogenic and natural disturbance lead to differing patterns of gene flow in the Rocky Mountain tailed frog, *Ascaphus montanus*. *Biological Conservation* 143: 778-786.

Specht R.L. (1972). *The Vegetation of South Australia.* AB James, Government Printer, Adelaide, SA.

Stephens P.A., Sutherland W.J. and Freckleton R.P. (1999). What is the Allee effect? *Oikos* 87: 185-190.

Stow A., Silberbauer L., Beattie A.J. and Briscoe D.A. (2007). Fine-scale genetic structure and fire-created habitat patchiness in the Australian allodapine bee, *Exoneura nigrescens* (Hymenoptera: Apidae). *Journal of Heredity* 98: 60-66.

Stow A.J., Sunnucks P., Briscoe D.A. and Gardner M.G. (2001). The impact of habitat fragmentation on dispersal in Cunningham's skink (*Egernia cunninghami*): evidence from allelic and genotypic analyses of microsatellites. *Molecular Ecology* 10: 867-878.

Sumner J., Rousset F., Estoup A. and Moritz C. (2001). 'Neighbourhood' size, dispersal and density estimates in the prickly forest skink (*Gnypetoscincus queenslandiae*) using individual genetic and demographic methods. *Molecular Ecology* 10: 1917-1927.

Sutton J.T., Nakagawa S., Robertson B.C. and Jamieson I.G. (2011). Disentangling the roles of natural selection and genetic drift in shaping variation at MHC immunity genes. *Molecular Ecology* 20: 4408-4420.

Teasdale L.C., Smith A.L., Thomas M., Whitehead C.A. and Driscoll D.A. (in review). Detecting invertebrate responses to fire depends on sampling method and taxonomic resolution in an Australian mallee woodland. *Austral Ecology*.

Templeton A.R., Brazeal H. and Neuwald J.L. (2011). The transition from isolated patches to a metapopulation in the eastern collared lizard in response to prescribed fires. *Ecology* 92: 1736-1747.

Templeton A.R., Robertson R.J., Brisson J. and Strasburg J. (2001). Disrupting evolutionary processes: the effect of habitat fragmentation on collared lizards in the Missouri Ozarks. *Proceedings of the National Academy of Science, USA*. 98: 5426-5432.

Thomas C.D. (2000). Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 267: 139-145.

Travis J.M.J. (2003). Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270: 467-473.

Travis J.M.J. and Dytham C. (1999). Habitat persistence, habitat availability and the evolution of dispersal. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 266: 723-728.

Twidale C.R. and Campbell E.M. (1985). The form of the land surface. In: *Natural history of Eyre Peninsula.* (eds. Twidale CR, Tyler MJ, Davies M). Royal Society of South Australia, Adelaide, SA.

Vilà-Cabrera A., Saura-Mas S. and Lloret F. (2008). Effects of fire frequency on species composition in a Mediterranean shrubland. *Écoscience* 15: 519-528.

Welsh A.H. (1996). *Aspects of Statistical Inference* John Wiley & Sons, Inc., New York.

Westgate M.J., Driscoll D.A. and Lindenmayer D.B. (2012). Can the intermediate disturbance hypothesis and information on species traits predict anuran responses to fire? *Oikos*: DOI 10.1111/j.1600-0706.2011.19863.x.

White P.S. and Pickett S.T.A. (1985). Natural disturbance and patch dynamics: an introduction. In: *The Ecology of Natural Disturbance and Patch Dynamics.* (eds. Pickett STA, White PS), pp. 3-13. Academic Press, San Diego, USA.

Williams J.R., Driscoll D.A. and Bull C.M. (2011). Roadside connectivity does not increase reptile abundance or richness in a fragmented mallee landscape. *Austral Ecology.*

Wilson S. and Swan G. (2010). *A Complete Guide to Reptiles of Australia*, 3 edn. New Holland, Sydney.

Wilson T.L., Johnson E.J. and Bissonette J.A. (2009). Relative importance of habitat area and isolation for bird occurrence patterns in a naturally patchy landscape. *Landscape Ecology* 24: 351-360.

Woinarski J.C.Z., Legge S., Fitzsimons J.A., Traill B.J., Burbidge A.A., Fisher A., Firth R.S.C., Gordon I.J., Griffiths A.D., Johnson C.N., McKenzie N.L., Palmer C., Radford I., Rankmore B., Ritchie E.G., Ward S. and Ziembicki M. (2011). The disappearing mammal fauna of northern Australia: context, cause, and response. *Conservation Letters* 4: 192-201.

Wright S. (1943). Isolation by distance. *Genetics* 28: 114-138.

Zuur A.F., Ieno E.N., Walker N.J., Saveliev A.A. and Smith G.M. (2009). *Mixed effects models and extensions in ecology with R.* Springer, New York.

6.8 Supporting material

6.8.1 Nephrurus stellatus *sample and site information*

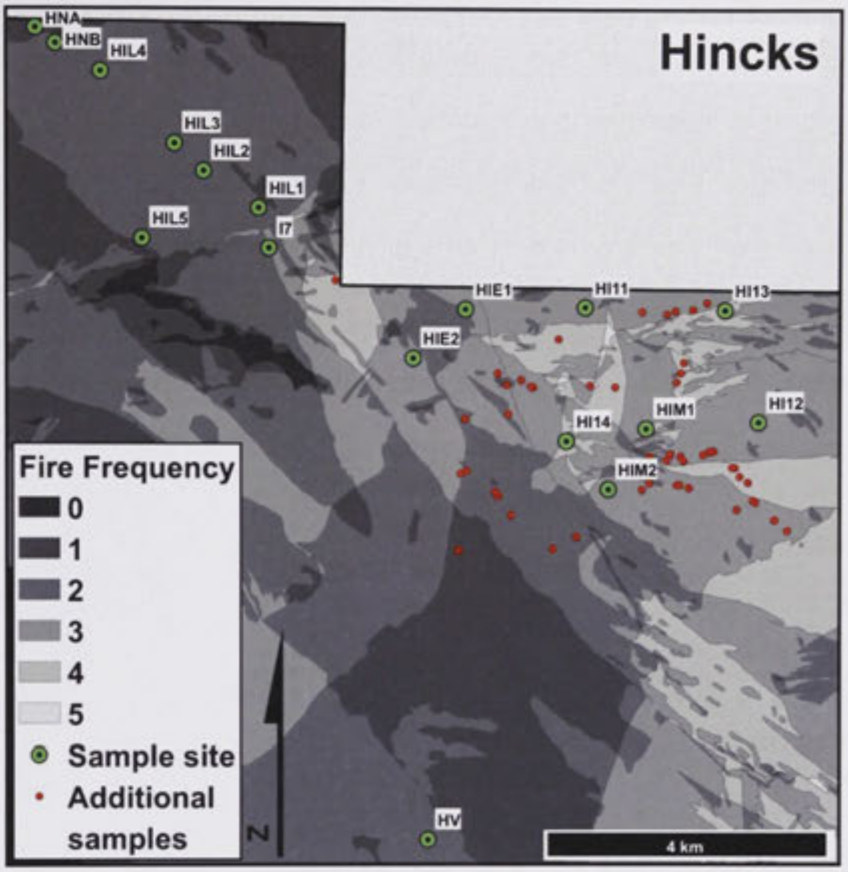
Table S6.1 DNA was sampled at 39 sites spanning 0.7 to 57 years since fire in the habitat. Additional samples were collected between the sites at Hincks and Pinkawillinie (see also Fig. 6.1). DNA was collected over six field seasons, but 93 % of samples were collected in the final three seasons (4-6). Season one was Dec 2004 – Feb 2005 and season six was Nov 2009 – Feb 2010.

Reserve	Site	N	Last fire	Seasons DNA collected	Collection method
Hincks	HIE1	48	2006	5-6	Pitfall grid
	HIE2	78	2006	5-6	Pitfall grid
	HIM1	95	1999	5-6	Pitfall grid
	HIM2	85	1999	5-6	Pitfall grid
	HI1	5	1966	4-6	Pitfall grid
	HI2	5	1966	4-5	Pitfall grid
	HI3	4	1966	5-6	Pitfall grid
	HI4	9	1966	4-6	Pitfall grid
	HI5	7	1966	4-6	Pitfall grid
	I7	10	1977	3-4	Pitfall transect
	HI11	15	1999	4	Manual
	HI12	21	1999	4	Manual
	HI13	18	1999	4	Manual
	HI14	26	1999	4	Manual
	HNA	3	1953	6	Manual
	HNB	9	1966	6	Manual
	HV	5	1977	6	Manual
	Additional samples	1	1977	5	Manual
		38	1999	5	Manual
		12	2006	4-5	Manual
Total		**494**			
Pinkawillinie	PE1	22	2005	5-6	Pitfall grid
	PE2	27	2005	5-6	Pitfall grid
	PM1	40	2001	5-6	Pitfall grid
	PM2	38	2001	5-6	Pitfall grid
	PL1	2	1960	6	Pitfall grid
	PL2	5	1960	6	Pitfall grid
	PL3	3	1960	5	Pitfall grid
	PL4	3	1960	5-6	Pitfall grid
	P4	12	2005	4	Pitfall transect
	P2	12	2001	4	Pitfall transect
	P7	13	1986	3-4	Pitfall transect
	P8	10	1986	3-4	Pitfall transect
	Additional samples	16	2005	4-5	Manual
		9	2001	5	Manual

Reserve	Site	N	Last fire	Seasons DNA collected	Collection method
		4	1986	4-5	Manual
Total		**216**			
Munyaroo	M1	10	1990	1-2	Pitfall transect
	M2	4	1990	1-2	Pitfall transect
	M3	6	1960	1-2	Pitfall transect
	M4	12	1960	1-2	Pitfall transect
Total		**32**			
Heggaton	N1	4	1997	4	Pitfall transect
	N3	5	1960	1-4	Pitfall transect
	N4*	1	1960	1	Pitfall transect
	S2	8	2001	3-4	Pitfall transect
	S3	1	1960	4	Pitfall transect
	S4	3	2006	3-4	Pitfall transect
Total		**22**			
Grand total		**764**			

* The sample from this site was collected before the 2006 fire at N4 shown in Figure 6.1. This, and two samples from N3 also collected before the 2006 fire, were removed from the landscape resistance analysis so that all samples in the analysis were collected after all fires in each reserve.

Fig. S6.1 A complex fire history at Hincks meant we were able to examine effects of fire frequency in addition to time since fire. Values of fire frequency that were used in the spatial model are shown in the map.



6.8.2 Genetic clusters in Nephrurus stellatus.

STRUCTURE identified two or three genetic clusters in the overall sample and GENELAND identified three (Fig. S6.2). Both methods identified a single cluster in the samples from each reserve separately except that three clusters were identified by GENELAND for Heggaton (Fig. S6.2). However, individuals at Heggaton were assigned with equal probability to each of the three clusters (Fig. S6.3) meaning the results were not reliable for this reserve.

Fig. S6.2 The number of genetic clusters (*K*) in the overall data set and for each reserve separately. Probability values for each *K* from the STRUCTURE results are shown in the left column, and the frequency of each *K* from the GENELAND results are on the right.

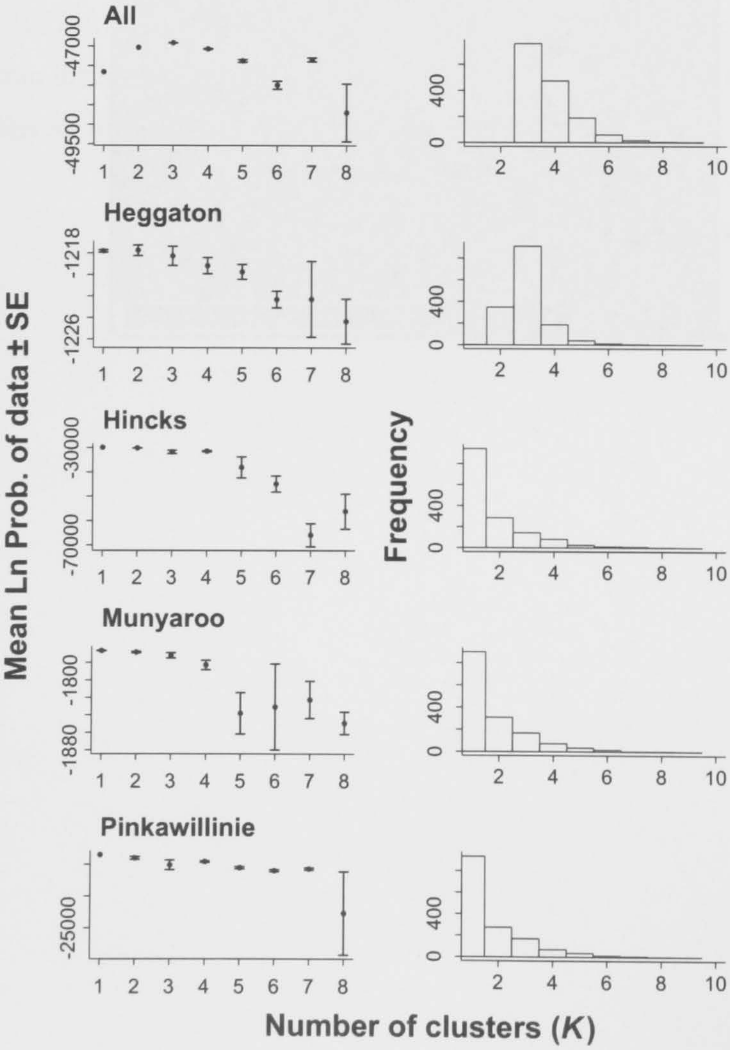
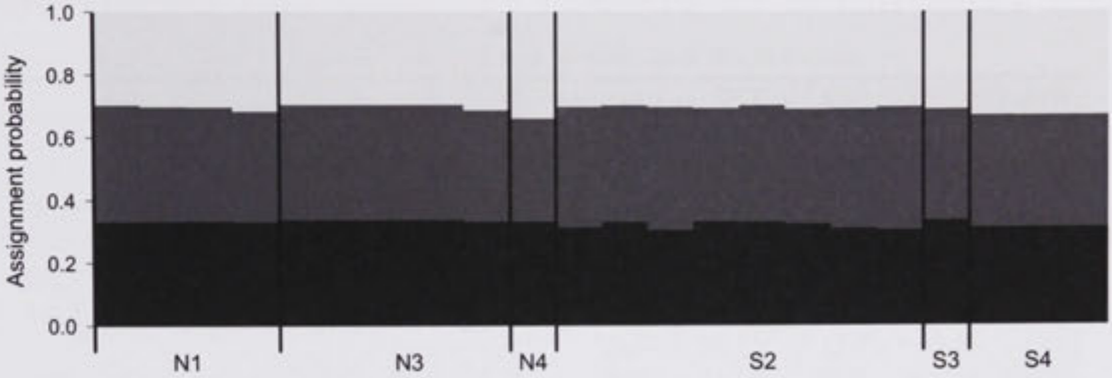


Fig. S6.3 Although three clusters were identified in the sample from Heggaton, each individual was assigned to each of the three clusters with equal probability, meaning the results were not reliable for this reserve.

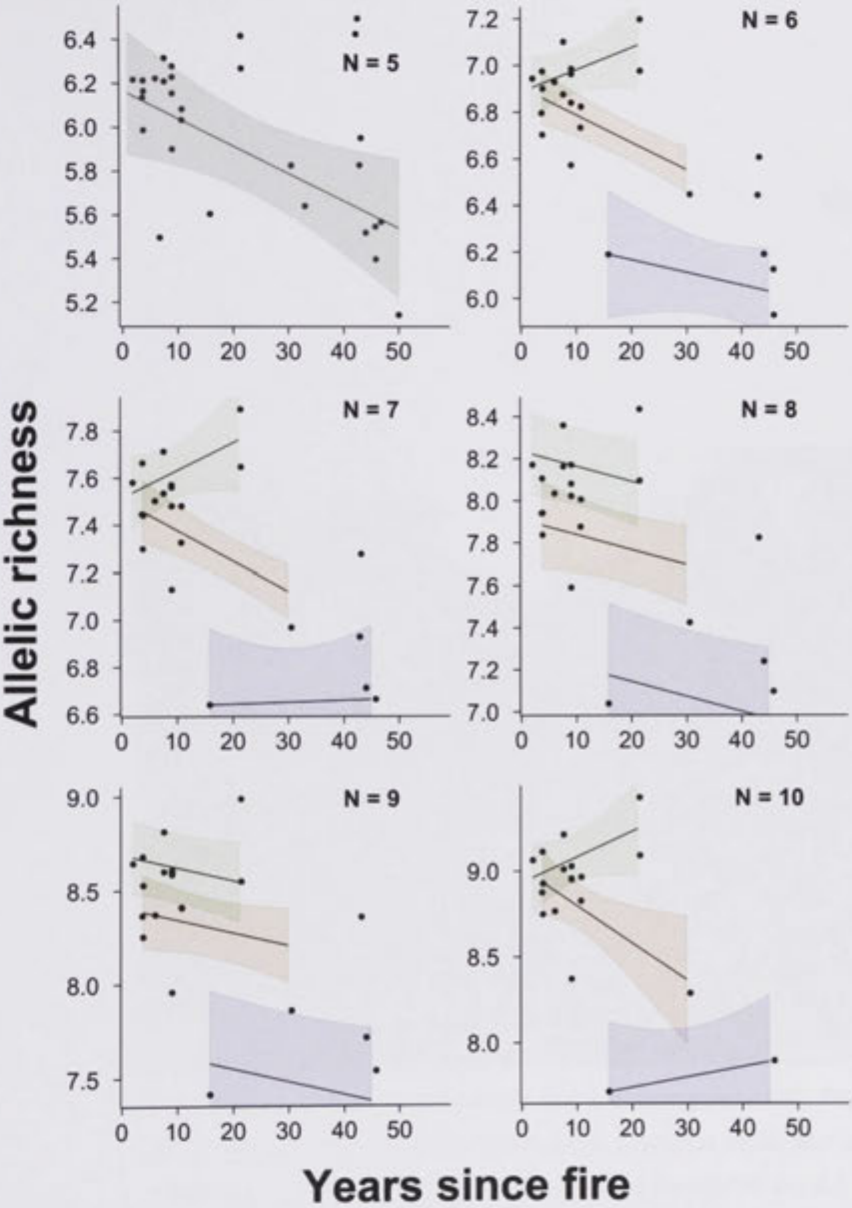


6.8.3 Fire and reserve effects on allelic richness.

Table S6.2 Sites with > 5 individuals were used in the analysis of allelic richness (AR) which was standardised to sample sizes of 5-10. The time since fire (TSF), last fire, and sample size (N) are shown for each site.

Reserve	**Site**	**TSF**	**Last fire**	**N**						
					5	**6**	**7**	**8**	**9**	**10**
Hincks	HI1	42.50	1966	5	6.50	-	-	-	-	-
	HI11	9.00	1999	15	5.90	6.57	7.13	7.59	7.96	8.37
	HI12	9.00	1999	21	6.23	6.96	7.56	8.08	8.61	9.03
	HI13	9.00	1999	18	6.28	6.99	7.57	8.17	8.60	8.96
	HI14	9.00	1999	26	6.16	6.84	7.48	8.02	8.59	8.95
	HI2	42.20	1966	5	6.43	-	-	-	-	-
	HI4	43.11	1966	9	5.96	6.61	7.28	7.82	8.36	-
	HI5	42.86	1966	7	5.83	6.45	6.93	-	-	-
	HIE1	3.81	2006	48	5.99	6.70	7.30	7.84	8.25	8.75
	HIE2	3.83	2006	78	6.17	6.90	7.44	7.94	8.53	8.93
	HIM1	10.71	1999	95	6.04	6.74	7.33	7.88	8.41	8.83
	HIM2	10.78	1999	85	6.08	6.82	7.48	8.01	8.41	8.97
	HNB	44.00	1966	9	5.52	6.19	6.71	7.24	7.71	-
	HV	33.00	1977	5	5.64	-	-	-	-	-
	I7	30.50	1977	10	5.83	6.45	6.97	7.43	7.86	8.29
Pinkawillinie	P2	6.00	2001	12	6.22	6.93	7.50	8.04	8.37	8.77
	P4	2.00	2005	12	6.22	6.94	7.58	8.17	8.65	9.06
	P7	21.46	1986	13	6.27	6.98	7.65	8.10	8.55	9.09
	P8	21.40	1986	10	6.42	7.20	7.89	8.44	8.99	9.43
	PE1	3.77	2005	22	6.21	6.98	7.66	8.11	8.68	9.11
	PE2	3.67	2005	27	6.14	6.80	7.45	7.94	8.37	8.88
	PL2	50.00	1960	5	5.14	-	-	-	-	-
	PM1	7.58	2001	40	6.21	6.88	7.54	8.16	8.60	9.01
	PM2	7.58	2001	38	6.32	7.10	7.71	8.36	8.81	9.21
Munyaroo	M1	15.80	1990	10	5.61	6.19	6.64	7.04	7.42	7.71
	M3	45.83	1960	6	5.40	5.93	-	-	-	-
	M4	45.75	1960	12	5.55	6.13	6.66	7.10	7.54	7.89
Heggaton	N3	46.80	1960	5	5.57	-	-	-	-	-
	S2	6.75	2001	8	5.50	6.06	6.54	6.93	-	-

Fig. S6.4 Time since fire (TSF) and reserve effects on allelic richness (AR) and the effect on changing the sample size (and thus the number of sites in the analysis). There was a main effect only of TSF when N = 5. When N = 6, 7, and 10 there were main and interactive effects of TSF and reserve. When N = 8 and 9 there were main effects of reserve on AR only. Model estimates and 95 % confidence intervals (Pinkawillinie = green, Hincks = pink, Munyaroo = purple) are shown over the raw data.



Chapter 7

Spatial and temporal variation in genetic structure of lizards in landscapes with complex fire mosaics

Research Paper

Co-authors:
C. Michael Bull
Michael G. Gardner
Don A. Driscoll

Triodia irritans *in an area at Hincks that last burned in 1966.* Triodia *grasses are essential habitat for the skink* Ctenotus atlas, *and are also used for shelter by the agamid* Amphibolurus norrisi *(Photo A.L. Smith, taken Feb 2009 at the site "HI5").*

7.1 Abstract

Fire mosaics are often assumed to benefit biodiversity, but little is known about how fire regimes affect dispersal and population genetic structure of animal species in fire prone regions. We conducted a replicated, spatio-temporal landscape genetics study to investigate the effects of complex fire mosaics on two Australian woodland lizard species (*Amphibolurus norrisi* (Agamidae) and *Ctenotus atlas* (Scincidae)). Both species decline in abundance after fire, but their population response to habitat succession varies regionally. Using Bayesian clustering (STRUCTURE and GENELAND) we found little genetic structure across the study landscapes, indicating high gene flow. However, analysis of landscape resistance showed that gene flow in *A. norrisi* was constrained by fire regimes (characterised by time since fire (TSF) and fire frequency), topography, and population density. In *A. norrisi*, gene flow and genetic diversity were higher in recently burnt than long unburnt habitats possibly from a disruption of stable social or territory structure. A longitudinal sampling regime revealed that fire eliminated spatial landscape-scale genetic structure in *A. norrisi* at one location, possibly because of increased immigration of "refugees" fleeing to unburnt habitat. Genetic diversity increased with TSF in *C. atlas*, even though there were no detectable effects of landscape features on gene flow. Increasing population size with time since fire may promote genetic diversity in *C. atlas*. Our results revealed complex relationships between gene flow, genetic diversity and population density that help explain population responses to fire regimes in the two lizard species. Such studies are necessary for understanding how fire mosaics will affect the dispersal and genetic structure of animals in fire prone ecosystems.

7.2 Introduction

Fire is a natural driver of ecological change, but modern changes in land use have altered fire regimes in ecosystems around the world (Franklin et al. 2008; Butz 2009; Moreira et al. 2011). Some animal species are threatened by recent increases in the extent and frequency of fire (Lyet et al. 2009; Sanz-Aguilar et al. 2011), while others decline where fire has become less frequent (Templeton et al. 2011). The species most at risk of decline under inappropriate fire regimes are "fire-specialists", i.e. those which specialise on a specific post-fire successional stage (Driscoll & Henderson 2008).

Different fire-specialists reach their peak abundance at different stages of the succession, meaning that community structure changes with increasing time since fire (Fox 1982; Letnic et al. 2004; Langlands et al. 2011). To cater for these changes, management agencies often use prescribed burning and/or fire suppression to create a "fire mosaic" under the assumption that successional diversity in vegetation will benefit biodiversity overall (Parr & Andersen 2006; Cushman et al. 2008). However, there is little understanding of the spatial and temporal scales at which fire mosaics will allow animal species to persist in a landscape (Bradstock et al. 2005; Clarke 2008).

Fire, or lack of fire, has the potential to fragment suitable habitat for some animal species (Templeton et al. 2001) because changes in habitat structure can affect their movement, dispersal and gene flow (Schmuki et al. 2006; Levy et al. 2010; Prevedello et al. 2010). When gene flow is restricted, genetic diversity and population fitness may decline, increasing the extinction risk to fragmented populations (Frankham 1997). Quantifying gene flow and genetic diversity across fire mosaics is an efficient way to determine if a pattern of fire events has resulted in dispersal barriers for fire-specialist animals. However, this has only recently received research attention (Murphy et al. 2010; Spear & Storfer 2010; Schrey et al. 2011). A comprehensive analysis of dispersal barriers must also consider other factors that influence gene flow such as population density (Konvicka et al. 2012), topography (Cushman et al. 2006), and geographic distance (Wright 1943).

Dispersal is a key factor influencing recolonisation after fire. If local extinction follows fire, dispersal from surrounding unburnt habitat is essential for recolonisation (Holland & Bennett 2011) and the rate of recolonisation by a species might depend on its dispersal ability (van Nouhuys & Hanski 2002). Dispersal may be less important if population recovery is initiated by survivors from the fire (Peakall & Lindenmayer 2006; Banks et al. 2011). Understanding the mode of recolonisation or population growth from survivors is necessary to accurately interpret population changes after fire and has implications for the spatial scales at which fire mosaics are managed.

Displacement following habitat disturbance can alter social and mating systems and thus the genetic structure of animal populations (Brockhurst et al. 2007; Walker et al. 2008; DiBattista et al. 2011; Schrey et al. 2011). Fire can also affect population structure in the areas surrounding burnt habitat if there is increased immigration of displaced animals into those areas (Banks et al. 2012). Landscape genetics offers a spatial examination of how fire affects animal population structure and dispersal by combining geographic information with multi-locus DNA data (Spear & Storfer 2010). However, untangling effects of long term habitat succession from effects of an initial displacement after fire may be difficult with "snap-shot" space-for-time studies (Porter 1999; Driscoll & Hardy 2005). Monitoring change in population structure over time is a better way to assess the impact of fire on animal populations, but such longitudinal data are typically difficult to obtain (Driscoll et al. 2010). Combining spatial and temporal sampling approaches may provide an efficient and informative method for examining animal population structure under complex fire regimes.

In this study we used a spatio-temporal sampling design and landscape genetics analyses to investigate initial and long term impacts of fire regimes on the population structure of two lizard species (*Amphibolurus norrisi* (Agamidae) and *Ctenotus atlas* (Scincidae)). The abundance of both species declines immediately after fire, but their population recovery varies regionally and involves factors other than simply time since fire (Driscoll & Henderson 2008; Driscoll et al. 2012). We therefore replicated our study regionally across four landscapes; a necessary but often overlooked approach in landscape genetics (Short Bull et al. 2011). We characterised fire regimes by fire frequency and time since fire and investigated effects of population density and topography on gene flow. Understanding and comparing how fire affects dispersal, population structure and recolonisation in the two lizard species will provide insights into the mechanisms behind their variable population responses to fire. Towards this goal, we asked three specific questions:

1. Do fire regimes, topography, and population density influence gene flow and genetic diversity in each of the two lizard species?
2. What is the immediate effect of fire in a landscape on the population structure of lizards?
3. Is post-fire recolonisation facilitated by survivors, or by immigration from unburnt habitat?

Our study combined space-for-time sampling to understand long-term effects of fire regimes on genetic structure, and longitudinal sampling over six years to answer questions about the initial impacts of fire and recolonisation. Overall, we sought to determine if complex fire mosaics created dispersal barriers in the two lizard species, and we sought to understand the mechanisms behind their successional responses after fire.

7.3 Methods

7.3.1 Study region & target species

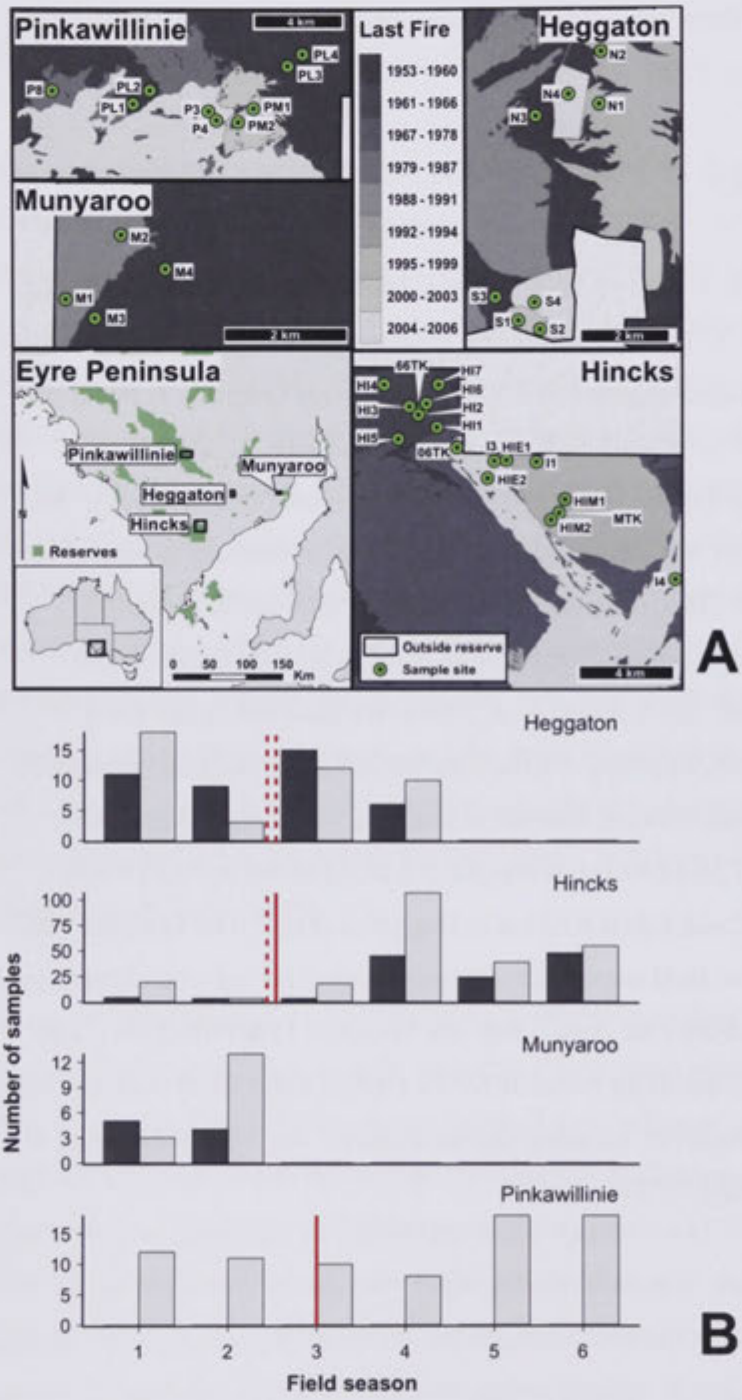
The study took place in four conservation reserves on the Eyre Peninsula, South Australia (Fig. 7.1a): Hincks Wilderness Area (33°45' S, 136°03' E; 66,658 ha), Pinkawillinie Conservation Park (32°54' S, 135°53' E; 130,148 ha), Munyaroo Conservation Park (33° 21' S, 137° 12' E; 20,139 ha), and Heggaton Conservation Reserve (33°22' S, 136°31' E; 6,476 ha). The region is semi-arid, with an average annual rainfall of 340 mm at Hincks, 303 mm at Pinkawillinie, 296 mm at Munyaroo, and 361 mm at Heggaton. The main topographic features are white sand dunes, occurring in either large, parabolic fields or longitudinal ridges interspersed by hard, reddish-brown swales (Twidale & Campbell 1985). The reserves are dominated by mallee vegetation which is characterised by multi-stemmed *Eucalyptus spp*., predominantly *E. costata*, and *E. socialis*, associated with the shrubs *Melaleuca uncinata* and *Callitris verrucosa*, and the spiky hummock grass *Triodia irritans* (Specht 1972; Robinson & Heard 1985). Summer lightning is the most common ignition source of mallee which typically results in large, severe wildfires on a decadal time scale (Bradstock & Cohn 2002).

The semi-arboreal dragon *Amphibolurus norrisi* (Agamidae) has a regionally variable response to fire, reaching its peak abundance 5-10 years after fire at Hincks, and more than 30 years after fire at Heggaton (Driscoll & Henderson 2008). The driver of this regional variation is currently unknown (Driscoll & Henderson 2008). *Ctenotus atlas* (Scincidae) is dependent on habitat provided by grasses of *Triodia* species (Pianka 1969b). Densities of *Triodia* vary regionally in relation to factors such as rainfall and grazing pressure that interact with fire regimes (Driscoll et al. 2012), but *Triodia spp.* generally reach their peak abundances approximately 30 years after fire (Haslem et al. 2011). *Ctenotus atlas* similarly peaks in abundance late in the post-fire succession at some locations (Smith et al. Chapter 3). Most *Triodia* species are associated with deep, sandy soils (Pianka 1972; Cohn 1995; Williams et al. 2011), so *C. atlas* may be more common at higher elevations that have greater sand depth. Sandy plains and dunes were used more often than swales in a radio-tracked sample (N = 35) of *A. norrisi* at Hincks (South 2010). Variation in elevation may therefore influence gene flow in both species if, for example, they disperse preferentially on dunes. *Amphibolurus norrisi* and *C. atlas* are both common in mallee habitats of southern Australia (Wilson & Swan 2010), but *A. norrisi* does not occur as far north as Pinkawillinie so samples for this species came from three reserves only (Fig. 7.1b).

7.3.2 Overview of study design

We collected a total of 177 *A. norrisi* and 377 *C. atlas* DNA samples, from 38 sites (*A. norrisi* = 26 sites, *C. atlas* = 31 sites), representing habitats spanning four days to 49 years after fire (Fig. 7.1a, Supporting material 7.8.1). To answer Question 1, about the influence of landscape features on gene flow and genetic diversity, we used these samples in a series of population and landscape genetics analyses (details below). We aimed to quantify the effect of fire on gene flow at spatial scales relevant to natural and prescribed fires in the mallee (Bradstock & Cohn 2002) and relevant to commonly reported extents of genetic structure in lizards (Stow et al. 2001; Sumner et al. 2001; Berry et al. 2005; Hoehn et al. 2007; Smith et al. 2009). We used individual-level analyses to quantify gene flow, avoiding arbitrary definitions of population boundaries. The mean (and range) distance between individual samples, including samples from within the same site, was 4.2 (0-15.4) km at Hincks, 5.3 (0-12.0) km at Pinkawillinie, 0.5 (0-1.8) km at Munyaroo, and 2.2 (0-6.6) km at Heggaton (Fig. 7.1a). Samples were collected over six consecutive field seasons (the spring/summer period when lizards in the mallee are most active), from Dec 2004 – Feb 2005 (season 1) to Nov 2009 – Feb 2010 (season 6) (Fig. 7.1b, Supporting material 7.8.1). Hincks had a more complex fire history than the other three reserves, meaning our sample sites also spanned a range of fire frequencies (0-5 fires since 1953).

Fig. 7.1 (A) Samples were collected from 38 sites across fire mosaics in four conservation reserves on the Eyre Peninsula, South Australia. (B) *Amphibolurus norrisi* (dark grey) and *Ctenotus atlas* (light grey) samples were collected before and after prescribed fires (red dotted lines) and wildfires (red solid lines), beginning in December 2004 (field season 1).



Our first research question was addressed using all of the samples. Questions 2 and 3 were addressed using subsets of the overall sample, and took advantage of prescribed fires (sites I3, N4, and S4) and unplanned wildfires (sites I4, P3, and P4) that occurred during our six years of sampling (Fig. 7.1b, Supporting material 7.8.1). Question 2, about the initial impacts of fire, was addressed by analysing landscape genetic structure separately for samples collected before and after fire. We conducted this analysis only for Heggaton where we had an approximately equal number of samples from multiple sites across the landscape both before and after prescribed fires at N4 and S4 (Fig. 7.1b, Supporting material 7.8.1). Question 3, about recolonisation, was addressed using samples from five of the six sites that burnt during the study (I3, I4, N4, P3, P4), where samples were collected before and after the fires (Fig. 7.1b, Supporting material 7.8.1). Thus, Question 2 compares spatial genetic structure across the whole landscape before and after fire at Heggaton, while Question 3 examines potential temporal changes in genetic structure at fixed locations within Hincks, Heggaton and Pinkawillinie.

7.3.3 Field data & sample collection

Thirty-five of the 38 sample sites consisted of pitfall trap stations arranged in either transects or grids. At the remaining three sites individuals were hand-captured (Supporting material 7.8.1). The 18 transect sites had 22 pitfall traps arranged in pairs at 40 m intervals along a 400 m transect, with a 20 m drift fence intersecting each trap pair (Driscoll & Henderson 2008). The 17 grid sites had 25 pitfall traps in a 1 ha grid, with five rows of five traps spaced at 25 m intervals, each intersected by a 10 m drift fence (Smith et al. 2012). Traps consisted of a 20 litre bucket buried flush with the ground surface. Trapped animals could shelter in a half PVC pipe placed at the bottom of each bucket and covered with a wood block which also acted as a floating refuge in case of heavy rain. In each season, during three 5-15 day trapping periods, traps within each reserve were opened and closed at the same times and checked daily while open.

Lizards were given a unique toe-clip to identify individuals upon recapture (Funk et al. 2005) using a system where usually two toes, and never more than three were removed (Waichman 1992). At the grid sites a small amount of blood from the toe was stored on FTA paper (Whatman) as a DNA source. Tissue from the clipped toe was preserved as an additional DNA source in liquid nitrogen or 5 ml ethanol/physiological saline

(1:1). Captured animals were taken to a base for processing and released the following day, 5 – 10 m from the capture location.

7.3.4 Microsatellite DNA data

We extracted DNA from FTA paper following Smith and Burgoyne (2004). Where FTA samples were not available, DNA was extracted from the tissue sample using a modified Gentra kit (Qiagen). We amplified DNA using the microsatellite primers and protocol described by Smith et al. (2011). Samples were genotyped on an ABI 3730 instrument (Applied Biosystems) with the size standard GS500 (-250) LIZ and alleles were scored with GeneMapper 4.0 (Applied Biosystems).

Before conducting population and landscape genetics analyses, we tested whether our microsatellite loci met the assumptions of Hardy-Weinberg and linkage equilibrium using option 1 and 2 of the web version of GENEPOP 4.0.10 (Raymond & Rousset 1995). Sample sites with ≥ 10 individuals were used for theses analyses (8 sites for *A. norrisi* and 14 for *C. atlas*, Supporting material 7.8.1). We sequentially adjusted *P*-values for multiple tests in each sample site (Hochberg 1988) and discarded data from loci with spatially consistent patterns of disequilibrium. Our final panels consisted of 13 markers for *A. norrisi* (AmNo04, AmNo05, AmNo11, AmNo12, AmNo18, AmNo20, AmNo25, AmNo26, AmNo29, AmNo30, AmNo36, AmNo37, AmNo39) and nine for *C. atlas* (CtAt02, CtAt03, CtAt08, CtAt09, CtAt12, CtAt15, CtAt18, CtAt24, CtAt30) (Smith et al. 2011).

7.3.5 Population genetic structure

We examined population genetic structure in *A. norrisi* and *C. atlas* across the four reserves on the Eyre Peninsula, and then separately within each of our study landscapes (the individual reserves). We included genotypes from all individual lizards in this analysis to help us answer all three of our research questions. If population genetic structure was related to spatial fire and topographic features it would help to identify barriers to gene flow (Question 1). Temporal changes in genetic structure following fire may also be evident from these analyses. For example, changes in spatial genetic structure at Heggaton following fire may indicate displacement of individuals following fire (Question 2) (e.g. Banks et al. 2012). Genetic differentiation corresponding to preand post-fire samples at fixed locations may indicate that recolonisation was facilitated by immigration, rather than survivors of the fire (Question 3).

For each data set we used two different Bayesian clustering models. First, we used a non-spatial model implemented in STRUCTURE 2.3.2. This uses a Markov-chain Monte Carlo (MCMC) method to identify the number of clusters (K) in a sample at Hardy-Weinberg equilibrium, and assign each individual probabilistically to a cluster (Pritchard et al. 2000). Second, we used a spatial MCMC model implemented in GENELAND 3.3.0 which is similar to STRUCTURE, but includes geographic coordinates for each individual (Guillot et al. 2005). This makes GENELAND more sensitive to weak genetic structure because spatially clustered individuals have a higher probability of being in the same genetic cluster (Guillot et al. 2005).

We ran STRUCTURE using the admixture and correlated allele frequency models for 500,000 MCMC repetitions after a burn-in of 200,000. Five independent runs of each K from 1 to 8 were conducted. We inferred the number of clusters in each data set by selecting the K with the highest mean estimated model log-likelihood ($\ln\Pr(X|K)$) across the independent runs (Pritchard et al. 2000). We ran GENELAND for 500,000 MCMC repetitions and allowed K to vary between 1 and 10. The Dirichlet allele frequency model was used because the correlated allele frequency model can overestimate K (Guillot et al. 2005), and we found it was unstable in preliminary analyses. We set spatial uncertainty of the coordinates at a conservative estimate of 1000 m to allow for potentially large home ranges in the lizards. We discarded the first 125,000 repetitions and then inferred K from the mode of the posterior distribution. Five independent runs were conducted to check for consistency of results.

7.3.6 Landscape resistance

To examine the effect of fire regimes, topography and population density on gene flow in *A. norrisi* and *C. atlas* (Question 1), we developed a set of landscape resistance models based on five features we considered to be important to gene flow: isolation by distance, elevation, time since fire, abundance, and fire frequency (Table 7.1). The fire frequency model was tested for Hincks only as it had a more complex fire history than the other three reserves. We examined the relationship between each landscape resistance model and genetic distance between individual lizards as a measure of gene flow (more detail below). At Heggaton, we also explored the initial impact of fire on landscape genetic structure by analysing samples before and after the 2006 prescribed fires separately (Question 2). For analysis of the other three reserves, we included only samples collected after the most recent fire in each reserve. We compiled all landscape models on raster grids with 20 m resolutions in ArcMap 9.2 (ESRI). To estimate resistance from each model we used a method based on circuit theory which takes into account all possible pathways between individuals (McRae & Beier 2007). Thus, to account for potentially long-distance dispersal, we defined the extent of our study landscapes with a 5 km buffer around the samples for each of the four data sets.

Table 7.1 We tested models of landscape resistance based on five features we considered to be important to gene flow in *Amphibolurus norrisi* and *Ctenotus atlas*. The fire frequency model was tested for Hincks only.

Spatial model	**Grid cell values**	**Potential ecological importance**
Isolation by distance	1	Genetic distance can increase with geographic distance (Wright 1943).
Elevation	Metres above sea level	Sand dunes are the dominant elevational features in our study system (Twidale & Campbell 1985). Both species may have a preference for sand dunes as *A. norrisi* have been recorded more commonly on dunes than swales (South 2010) and *C. atlas* depend on *Triodia spp*. which occur on deep sands (Pianka 1972; Williams et al. 2011). Gene flow may be influenced by elevation (representing the topography of the dunes) if dunes affect their dispersal ability.
Time since fire	Number of years since most recent fire (1-54)	Marked changes in vegetation structure with time since fire occur at our study sites (Smith et al. 2012) and habitat structure can affect dispersal in lizards (Berry et al. 2005; Templeton et al. 2011).
Abundance	Mean no. captures predicted from time since fire (Smith et al. Chapter 3)	The suitability of habitat for lizards does not always change linearly with time since fire (Driscoll & Henderson 2008; Driscoll et al. 2012). Dispersal through unsuitable habitat may be inhibited (Prevedello et al. 2010; Shanahan et al. 2011) or promoted (Driscoll & Hardy 2005; Schtickzelle et al. 2007). Increased population density can influence gene flow (Stephens et al. 1999; Robinet et al. 2008).
Fire frequency	Number of fires since 1953 (0-5)	Fire can have cumulative effects on animal populations (Lindenmayer et al. 2008) either through demographic impacts of repeated burning (Westgate et al. 2012), or changes in habitat structure (Pausas & Lloret 2007) that might affect gene flow.

The isolation by distance (IBD) model produced a "flat" landscape and accounted for the extent of the study area (Lee-Yaw et al. 2009). Significant positive IBD would suggest that gene flow decreases with increasing geographic distance between sample locations. The elevation model tested if gene flow was inhibited or promoted by sand dunes – the dominant topographic features on the Eyre Peninsula (Table 7.1). Positive coefficients for the elevation model would indicate lower gene flow at higher elevations. For the time since fire (TSF) model, positive coefficients would indicate that the habitat becomes more resistant to gene flow with increasing time since fire in a linear way (Table 7.1). The abundance was based on the same spatial configuration as the TSF model but parameterised with the predicted abundance for a given TSF (more detail below). High values specified high resistance, so positive coefficients for this model would suggest reduced gene flow in habitats where the animals were most common. The abundance model allowed us to examine demographic or habitat related changes in gene flow with TSF where the population response to TSF was non-linear (Table 7.1). For the fire frequency model, positive coefficients would suggest that gene flow decreases with increased number of fires in a habitat (Table 7.1).

Our elevation data were sourced from the Shuttle Radar Topographic Mission one-second bare earth version of Australia (CSIRO 2011). Elevations were projected as points from WGS84 to GDA94 (Universal Transverse Mercator zone 53), then interpolated with ANUDEM (Hutchinson 2011) to create digital elevation models for our study landscapes. The three fire-related models were derived from two different polygon layers containing the extent and year of the most recent fire (time since fire and abundance models) and of all fires (fire frequency model) since 1953 (South Australian Department for Environment and Natural Resources). For the abundance model we used the mean number of captures predicted from time since fire (Smith et al. Chapter 3) which enabled us to parameterise areas we had not sampled. Estimates were available for Hincks and Pinkawillinie only, so we generated predictions for Munyaroo and Heggaton using data from pitfall trap surveys (Supporting material 7.8.2). We examined abundance models of gene flow only for locations where there was a significant response to time since fire.

For each spatial model we calculated landscape resistance between all pairs of individuals within each reserve using CIRCUITSCAPE 3.5.4 (McRae & Beier 2007). We used SPAGEDI 1.2 (Hardy & Vekemans 2002) to calculate genetic distance between all pairs of individuals as a_r, an individual analogue to F_{ST} / (1- F_{ST}) (Rousset 2000). We used regression of distance matrices (Legendre et al. 1994) to examine the relationship between genetic distance and landscape resistance for each spatial model separately. The MRM function in ecodist (Goslee & Urban 2007) for R 2.14 (R Development Core Team 2011) was used to fit the models, and *P*-values were generated with 10,000 simultaneous permutations of the rows and columns of the dependent variable matrix (Legendre et al. 1994). Our spatial fire data were restricted to the reserves but the buffers extended outside these areas. Thus, for each of the three fire-related models, we initially tested if the agricultural land outside the reserves had either high or low resistance to gene flow. Two different parameterisations for the agricultural land were tested using the minimum and maximum values from each landscape model. The model with the highest R^2 was then used in the main analysis. We examined additive effects of elevation and the fire-related models where P was < 0.05 for the single predictors. To do this, values in the raster grids were scaled between 1 and 10, values from the two grids were added together, and resistance for the additive data was calculated in CIRCUITSCAPE.

7.3.7 Genetic diversity

To determine if post-fire succession affected genetic diversity in our target species (Question 1), we analysed variation in two different diversity measures: site-level allelic richness (AR) and individual heterozygosity. We used standArich (Alberto 2006) in R to calculate AR standardised for sample size (N). It was only possible to thoroughly examine effects of time since fire on AR when N was small because many of our sites had small sample sizes. We thus calculated AR for N = 5 to include a wide range of times since fire. For comparison with larger sample sizes, we also calculated AR for N = 6 to 10, however as N increased, the number of sites included in the analysis decreased. For each N, we calculated the mean AR from 100 random samples from each site (Leberg 2002). We used linear mixed models in lme4 (Bates et al. 2011) to examine the effect of time since fire (TSF) on AR for each N. Because we sampled multiple sites within a single fire boundary we fitted fire (a factor naming individual fire events) as a random effect and TSF and reserve as fixed effects. We examined interactions between TSF and reserve for *C. atlas*, but not *A. norrisi* because all of its observations from Heggaton had the same TSF and there was only one observation from Munyaroo. To estimate the effect of TSF on individual genetic diversity we first calculated the proportion of typed loci that were heterozygous in each individual. We modelled heterozygosity with the same formulation as for AR (including interactive effects of TSF and reserve for both species), but also included site as an additional random term to account for potential dependence among individuals at the same site.

For both the AR and heterozygosity analyses, we calculated *P*-values using Wald tests (Welsh 1996). When the interactive term was not significant ($P > 0.05$) we removed it, and subsequently removed the factor reserve if it was not significant in the resulting model (Zuur et al. 2009). Parameter estimates and standard errors were obtained using the AICcmodavg package (Mazerolle 2011).

7.4 Results

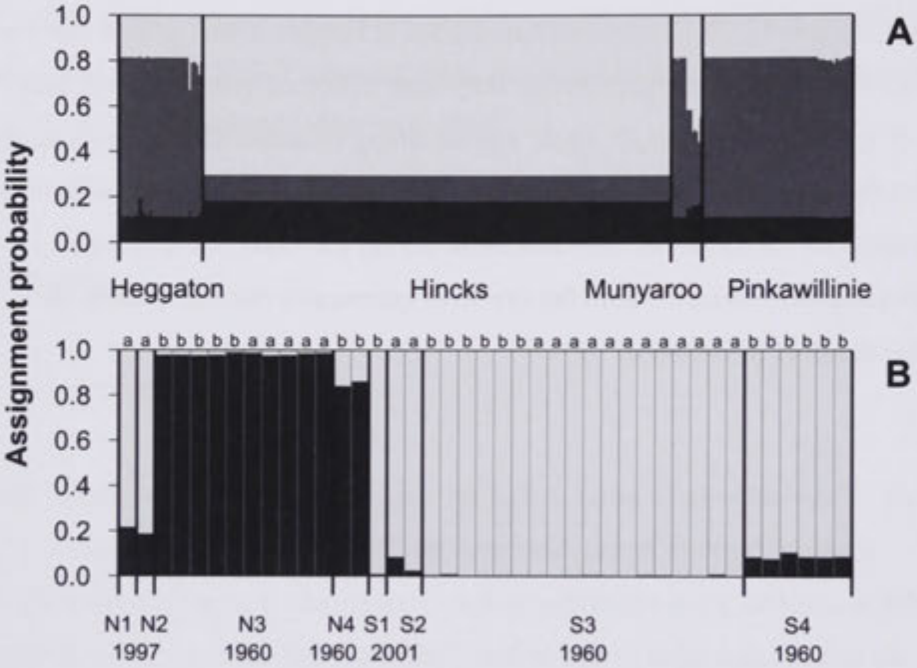
7.4.1 Genetic data properties

We produced microsatellite genotypes for 177 *A. norrisi* individuals at 13 loci and for 377 *C. atlas* individuals at 9 loci. There was evidence of Hardy-Weinberg disequilibrium in three *A. norrisi* loci, each at a different site (AmNo12 at HIM1, AmNo18 at HI7, and AmNo37 at HIM2) and in one *C. atlas* locus at one site (CtAt12 at N4 after the 2006 fire). For *A. norrisi* there was evidence of linkage disequilibrium in one locus pair at HI5 (AmNo05/AmNo20) and two locus pairs at S3 (AmNo36/AmNo37, and AmNo18/AmNo20) out of a total of 355 pairwise comparisons. There was no evidence for linkage disequilibrium in any of 299 pairwise comparisons of *C. atlas* loci. Given that there were no consistent patterns of disequilibrium across sites we considered all loci to be in Hardy-Weinberg and linkage equilibrium.

7.4.2 Genetic structure

At both spatial scales examined (i.e. across the Eyre Peninsula study region and separately within each of the study landscapes) STRUCTURE results indicated that all individuals within each species belonged to a single genetic cluster (Supporting material 7.8.3). The GENELAND results suggested that *C. atlas* individuals at Hincks were genetically differentiated from those at the other reserves (Fig. 7.2a, Supporting material 7.8.3). However, assignment probabilities were never > 71 % suggesting weak differentiation (Fig. 7.2a). One "ghost" cluster (Guillot et al. 2005) was also identified to which no individuals were assigned with the highest probability (Fig. 7.2a). GENELAND results from Heggaton indicated that *A. norrisi* individuals at N3 and N4 (last burned in 1960) were genetically differentiated from the other sites in that reserve (Fig. 7.2b). There was no differentiation across the fire mosaic at the southern Heggaton sites (Fig. 7.2b), thus no consistent genetic structure related to fire mosaics evident from this analysis (Question 1). The genetic differentiation at Heggaton was related more to the spatial location of samples, than whether they were collected before or after fires in that reserve (Fig. 7.2b) (Question 2). There was no strong evidence of genetic structure in any of the other data sets from individual reserves or across the Eyre Peninsula region (Supporting material 7.8.3). At the sites that burnt during the study, we found no evidence that samples collected before the fire were genetically distinct to samples collected after the fire (Question 3).

Fig. 7.2 Probabilities of assignment to genetic clusters identified by GENELAND (each bar represents an individual lizard). Differentiation between Hincks at the other reserves was evident for *C. atlas* (A) and a distinct cluster was formed by N3 and N4 within Heggaton for *A. norrisi* (B). For Heggaton (B), the site name and year of last fire is shown below the bars, and whether samples were collected before (b) or after (a) the prescribed fires is shown above the bars.



7.4.3 Landscape resistance

We found significant effects of landscape features on gene flow in all three reserves for *A. norrisi* (Table 7.2) but no significant effects for *C. atlas* (Supporting material 7.8.4). At Hincks, genetic distance in *A. norrisi* increased with increasing geographic distance, elevation, and fire frequency (Table 7.2). There was also a positive relationship between genetic distance and the additive model for elevation and fire frequency showing that these variables have a stronger combined influence on gene flow than either one considered alone (Table 7.2). Before the 2006 prescribed fires at Heggaton, all of the landscape features we examined explained significant variation in genetic distance of *A. norrisi* (Table 7.2). After the fires, these effects were no longer detected (Table 7.2). At Munyaroo the time since fire model had the only significant relationship, and showed increasing genetic distance with increasing time since fire (Table 7.2).

Table 7.2 The effect of landscape features on gene flow in *Amphibolurus norrisi*. Significant relationships ($\alpha = 0.05$) are shown in bold.

Model	Relationship	R^2	*P*-value
HINCKS (N = 120)			
Isolation by distance	**+**	**0.0069**	**0.001**
Elevation	**+**	**0.0061**	**0.001**
Time since fire	-	0.0002	0.764
Abundance	+	0.0047	0.090
Fire frequency	**+**	**0.0085**	**0.011**
Elevation + Fire frequency	**+**	**0.0069**	**0.008**
HEGGATON (Before 2006 fires, N = 20)			
Isolation by distance	**+**	**0.0278**	**0.023**
Elevation	**+**	**0.0249**	**0.033**
Time since fire	**+**	**0.0538**	**0.014**
Abundance	**+**	**0.0548**	**0.013**
Elevation + Time since fire	**+**	**0.0442**	**0.014**
Elevation + Abundance	**+**	**0.0446**	**0.013**
HEGGATON (After 2006 fires, N = 21)			
Isolation by distance	+	0.0171	0.167
Elevation	+	0.0189	0.156
Time since fire	+	0.0204	0.114
Abundance	+	0.0150	0.193
MUNYAROO (N = 9)			
Isolation by distance	+	0.0040	0.641
Elevation	+	0.0040	0.644
Time since fire	**+**	**0.2246**	**0.025**

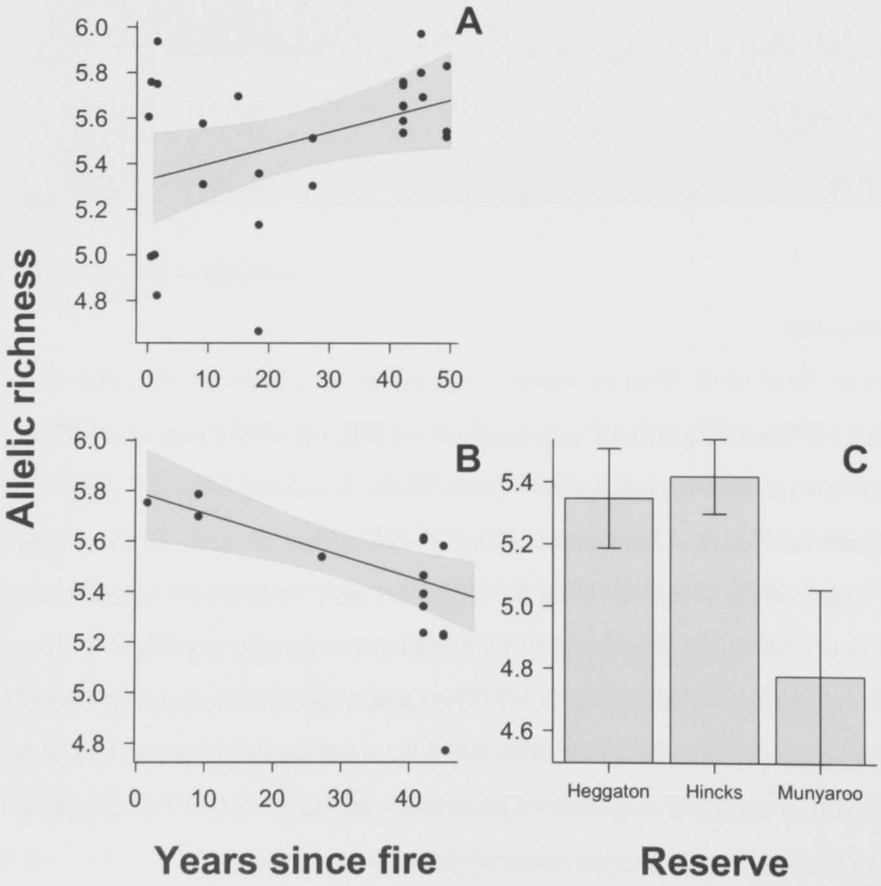
7.4.4 Genetic diversity

For both species, we found significant main effects of TSF on allelic richness (AR) for all sample size standardisations, except N = 7 and 10 for *C. atlas* (Table 7.3, Fig. 7.3a, b, Supporting material 7.8.5). Allelic richness increased with time since fire in *C. atlas* and decreased with TSF in *A. norrisi* (Fig. 7.3a,b). In *A. norrisi* there were also main effects of reserve on AR when N = 5 and 6, with Munyaroo having significantly lower AR than Hincks and Pinkawillinie (Fig. 7.3c). The reserve effect disappeared when N > 6 because it was driven by the site at Munyaroo (M3) which had only six individuals. There were no main or interactive effects of reserve on AR in *C. atlas*. There were no effects of TSF or reserve on individual heterozygosity in either species.

Table 7.3 *P*-values from linear mixed models to examine the effect of time since fire (TSF) and reserve on allelic richness in *Amphibolurus norrisi* and *Ctenotus atlas*.

N random	***A. norrisi***		***C. atlas***	
subsamples	**TSF**	**Reserve**	**TSF**	**Reserve**
5	0.003	< 0.001	0.037	-
6	0.003	0.004	0.017	-
7	< 0.001	-	0.087	-
8	0.001	-	0.002	-
9	0.016	-	0.002	-
10	0.021	-	0.069	-

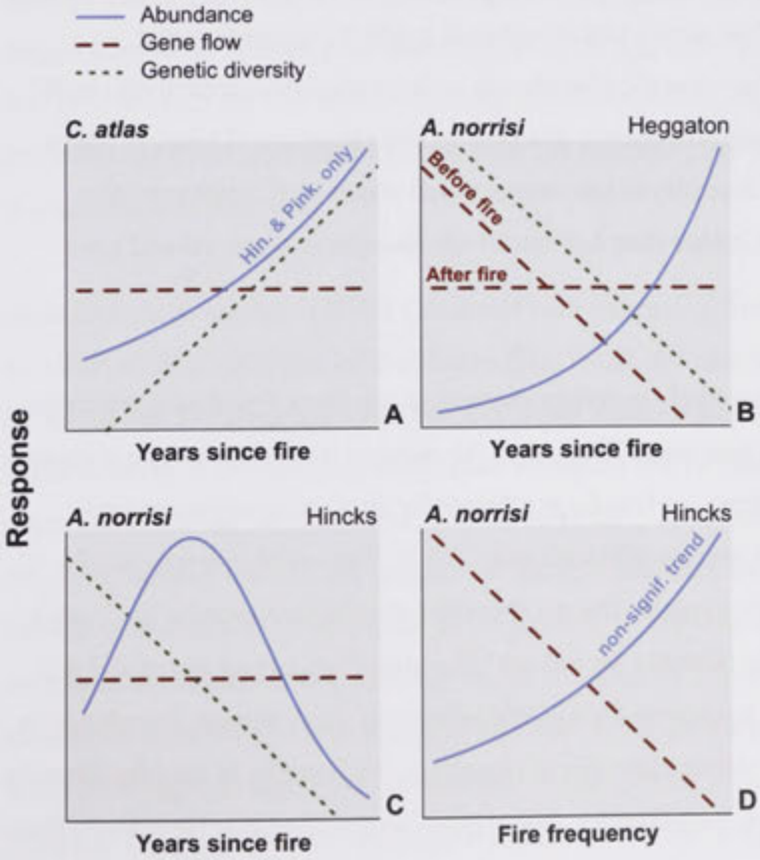
Fig. 7.3 Allelic richness (A) increased with time since fire in *Ctenotus atlas* and (B) decreased in *Amphibolurus norrisi*. (C) There was lower allelic richness in *A. norrisi* at Munyaroo than at the other reserves. Model estimates are shown over the raw data (A and B) and all results are from a standardised sample size of five individuals. Error bars are 95 % confidence intervals.



7.5 Discussion

We found complex relationships between fire regimes and genetic population structure in *Amphibolurus norrisi* and *Ctentous atlas* (summarised in Fig. 7.4). In answer to our first research question, we found that landscape features, including fire regimes, affected gene flow in *A. norrisi*, and that time since fire affected the genetic diversity of both lizard species. We detected a temporal change in landscape-scale genetic structure of *A. norrisi* at Heggaton, possibly reflecting an immediate impact of fire on the population structure (Question 2). There were no genetic changes following fire at fixed locations that would indicate recolonisation from immigration (Question 3) but detecting these changes would probably require stronger genetic structure than we found in our target species.

Fig. 7.4 A conceptual diagram showing relationships between fire regimes and abundance, gene flow, and genetic diversity in *Amphibolurus norrisi* and *Ctentous atlas*. Abundance curves are from Smith et al. (Chapter 3) and Supporting material 7.8.2.



7.5.1 Factors influencing gene flow & genetic diversity

Genetic diversity is usually higher in large than small populations because genetic drift, which reduces variability, is stronger when effective population sizes are small (Frankham 1996). Gene flow can maintain genetic diversity (Frankham 1997) so reductions in genetic diversity at neutral markers such as microsatellites may arise from either reduced effective population size and/or reduced gene flow. In *C. atlas*, we found higher genetic diversity at late successional stages where the skinks are usually more abundant (Fig. 7.4a). A similar result was found by Schrey et al. (2011) in a study of the Florida sand skink, another late-successional fire-specialist. In their study, skinks in recently burnt habitat had reduced allelic richness and increased variance in genetic diversity (Schrey et al. 2011). Increased genetic diversity in Florida sand skinks was driven by increases in population density and gene flow (Schrey et al. 2011). In *C. atlas* however, increased genetic diversity with time since fire was not accompanied by higher gene flow (Fig. 7.4a). This contrasts with most studies on lizards where gene flow and genetic diversity showed congruent responses to habitat variation (Sumner et al. 2004; Berry et al. 2005; Hoehn et al. 2007; Levy et al. 2010). Dubey and Shine (2010) however, found a positive relationship between genetic diversity and elevation in the Blue Mountains water skink that corresponded to changes in population size. They found no change in gene flow across this elevational gradient, suggesting that demographic instability from climatic disturbance or inter-specific competition could have reduced population size and genetic diversity at low elevations (Dubey & Shine 2010). The higher genetic diversity at late-successional stages in *C. atlas* may also relate to higher abundance, rather than habitat-driven changes in dispersal and gene flow.

Our results from *C. atlas* are likely to reflect changes in the grass *Triodia* on which the skinks depend, rather than time since fire *per se*. Abundance in *C. atlas* does not always respond to time since fire because *Triodia* is affected by interacting environmental factors such as rainfall and grazing (Driscoll et al. 2012). The variable response of *Triodia* following fire might explain why we observed abundance variation in *C. atlas* at Hincks and Pinkawillinie (Chapter 3), but not Heggaton (Supporting material 7.8.2; data from Munyaroo were too sparse for reliable inference). Even though abundance in *C. atlas* was not affected by time since fire at Heggaton, the increase in genetic diversity occurred across all reserves, including the four sample sites analysed at Heggaton. Thus, our results indicated an accumulation of genetic diversity over time even in the absence of changes in population density and gene flow. A simulation study (e.g. Schrey et al. 2011) may help to determine the relative contribution of population density, gene flow and unexplained variation on genetic diversity in *C. atlas*.

While genetic diversity increased with time since fire in *C. atlas*, the opposite pattern occurred in *A. norrisi*: sites with the longest time since fire had the lowest genetic diversity (Fig. 7.4b,c). At Heggaton this corresponded to a significant increase in abundance and a decrease in gene flow (before the 2006 fires) (Fig. 7.4b). A decrease in gene flow with time since fire was also found at Munyaroo. Changes in social or territorial behaviour with time since fire provide one explanation for these results. Territorial behaviour is common in agamid lizards (Martins 1994) and has been documented in the closely related *A. muricatus* (Peters & Ord 2003). In skinks, stable social organisation can constrain gene flow leading to fine-scale spatial genetic structure (Gardner et al. 2001; Stow & Sunnucks 2004; Fuller et al. 2005). Little is known about the relationship between social organisation and gene flow in agamids, but Griffiths (1999) suggested that home range size in the arboreal frillneck agamid is largely determined by its social and territory structure. Radio-tracking data (South 2010) showed that *A. norrisi* in 49 year old mallee at Heggaton had significantly smaller home ranges than those in three post-fire stages (43, 10, and three years since fire) at Hincks. It is possible that the low levels of genetic diversity in long unburnt areas at Heggaton represent the norm, and this increases after fire because gene flow increases through disrupted social structure.

Gene flow in *A. norrisi* at Hincks declined with increasing fire frequency, but there was no effect of time since fire or abundance (Fig. 7.4d). We also found additive effects of elevation and fire frequency, but the best fitting model was fire frequency alone. Unfortunately, it was difficult to separate effects of fire frequency from effects of time since fire at Hincks because these two variables were correlated (Supporting material 7.8.6). Why then, was the fire frequency model significant, but not the time since fire model? One explanation is that the fire frequency model was related to the non-linear change in abundance with time since fire at Hincks (see Supporting material 7.8.6). Our abundance model was designed to test this, and although it was not significant, it had a better fit to the data than the time since fire model (Table 7.2), giving some support to this idea. The fire frequency landscape had a more complex and patchy spatial configuration than the time since fire and abundance models (Supporting material 7.8.6). This patchiness might more accurately reflect variation in population density and therefore gene flow in *A. norrisi*. Alternatively, the decline in gene flow with increasing fire frequency could reflect variation in movement and dispersal ability because fire frequency can affect vegetation structure at a local scale (Pausas & Lloret 2007; Vilà-Cabrera et al. 2008).

The effect of fire frequency on animals is still poorly known (Clarke 2008; Driscoll et al. 2010), even though it may profoundly impact populations through demographic effects (e.g. repeated local extinctions) or changes in habitat structure. Animal population dynamics have been examined in landscapes with a wide range of fire frequencies where a widespread fire homogenised time since fire (e.g. Lindenmayer et al. 2008; Westgate et al. 2012). These kinds of landscapes are essential to untangle effects of time since fire and fire frequency and will be important for future studies investigating the influence of fire frequency on animal dispersal and gene flow.

Recently, landscape genetics analyses have revealed effects of topographic features, such as slope and elevation, on gene flow in many terrestrial animal species, particularly in montane systems (Storfer et al. 2010). In arid and semi-arid Australia, sand dunes have a strong influence on local abundances of many reptile species (Pianka 1969a; Pianka & Pianka 1976) through their interaction with *Triodia* species which usually occur on deep, sandy soils (Pianka 1972; Cohn 1995; Williams et al. 2011). Despite the prevalence of sand-dune/*Triodia* ecosystems in Australia and their influence on reptiles, we are unaware of any other studies that have investigated the effects of sand dune topography on dispersal and gene flow in lizards. In our study landscapes, higher elevations represented higher points on the sand dunes, thus deeper, sandy soil. Increasing elevation created resistance to gene flow in *A. norrisi* at Hincks and Heggaton (before the 2006 fires) suggesting that gene flow was lower on sand dunes than the in swales between the dunes. Preliminary radio-tracking (South 2010) suggested that *A. norrisi* use dunes more commonly than the inter-dune swales. Driscoll and Hardy (2005) showed that the related *A. nobbi* had elevated gene flow through cleared, agricultural land compared with nature reserves, and suggested that they might disperse rapidly through unsuitable habitat. It is possible that *A. norrisi* develop stable home ranges on dunes, but disperse rapidly through less sandy areas, leading to greater gene flow at lower elevations. However, more detailed field data about habitat use in *A. norrisi* are necessary to understand their association with topography.

7.5.2 Initial impacts of fire on genetic structure

Before two prescribed fires were conducted at Heggaton in 2006, all models of landscape resistance that we tested had significant effects on gene flow in *A. norrisi* (Fig. 7.4b). However, after fires these effects were no longer present, suggesting that gene flow was no longer restricted (Fig. 7.4b). Increases in gene flow following disturbance have also been observed in other species (DiBattista et al. 2011; Schrey et al. 2011; Banks et al. 2012). A late-successional pattern of isolation by distance was disrupted following fire in Florida sand skinks (Schrey et al. 2011). Fire eliminated fine-scale genetic structure of mountain brushtail possums and disrupted their social structure, while social cooperation in the surrounding unburnt habitat increased in response to an influx of immigrants from the burnt area (Banks et al. 2012). In *A. norrisi*, the post-fire change we observed occurred even though our samples were collected outside of the burnt areas at Heggaton (Supporting material 7.8.7). The change in genetic structure of *A. norrisi* following fire may therefore reflect an increase of "refugees" fleeing to unburnt habitat (Porter 1999). Continued investigation of changes in genetic structure following fire across multiple landscapes is necessary to thoroughly test this hypothesis.

7.5.3 Post-fire recolonisation

We did not observe any temporal genetic changes at fixed locations following fire that would indicate recolonisation from immigration. However, our genetic cluster analyses revealed generally high levels of gene flow in the two species, so detecting such changes would be difficult using this method (Berry et al. 2004). Studies of Australian bush rats, *Rattus fuscipes* have shown that both survivors (Peakall & Lindenmayer 2006; Banks et al. 2011) and short-distance (< 2 km) dispersers (Holland & Bennett 2011) contribute to population recovery following disturbance. Although we were not able to separate these mechanisms in this study, the ability to maintain high gene flow is likely to benefit the lizard species we studied in the face of temporal and spatial variation in fire regimes. This may be particularly important in cases where disturbance can completely eliminate the resident population (Peakall & Lindenmayer 2006).

7.5.4 Conclusions

Our study revealed complex relationships between fire regimes and genetic structure of two fire-specialist lizard species. None of the landscape resistance models we tested explained significant gene flow in *C. atlas*, suggesting that fire does not disrupt dispersal to a level that leaves a genetic signal. An alternative explanation is that the temporal scale of fires in relation to generation time may have been insufficient to detect any effects (Landguth et al. 2010). Since *C. atlas* depend on *Triodia spp.*, understanding how these grasses are affected by factors interacting with fire regimes (e.g. variation in climate and grazing pressure) is necessary to predict the persistence of animal species relying on *Triodia*. Gene flow in *A. norrisi* was significantly affected by topographic and fire-related landscape features, so the spatial scales at which fire mosaics are managed are likely to affect the dispersal and population structure of this species. Furthermore, genetic diversity was affected by post-fire habitat succession in both of our study species. Signals of neutral genetic diversity often correspond to adaptive variation (Sutton et al. 2011), meaning that variation in fire regimes could influence not only population density, but their potential fitness. The effect of fire regimes on the population structure of lizards varies between species, and within species at different locations. To cater for these complex patterns it is important that extreme management regimes such as complete fire suppression or widespread burning are avoided. Incorporating information about animal dispersal ability and population structure into fire response models (e.g. Bradstock et al. 2005) will help develop management practices that ensure species persistence in fire-prone landscapes.

7.6 Acknowledgements

Over 100 volunteers were involved in collecting samples for this project, and substantial field assistance was provided by Samantha Blight, Simone Dalgairns, Juliana Lazzari, Kevin Mayes, Andrew Murphy, Sally South, and Catherine Whitehead. Many thanks to Kathy Saint, Terry Bertozzi, and Steve Donnellan at the South Australian Museum for assistance with molecular data collection. The South Australian Department of Environment and Natural Resources (SA DENR), particularly Joe Tilley from the Pt Lincoln branch, provided logistical support in the field. John Stein kindly created digital elevation models and gave advice on spatial data analysis. Ingrid Stirnemann and David

Wong provided useful advice on an early draft of the manuscript. This research was supported by funds from the Australian Research Council, the Wildlife Conservation Fund, The Sir Mark Mitchell Research Foundation, The Lirabenda Endowment Fund, and the Ecological Society of Australia. We worked under scientific permit S25589 (SA DENR) and animal ethics permit E256 (Flinders University).

7.7 References

Alberto F. (2006). *standArich: an R package to estimate population allelic richness using standardized sample size.* CCMAR, University of the Algarve, Portugal. http://www.ccmar.ualg.pt/maree/software.php?soft=sarich.

Balkenhol N., Waits L.P. and Dezzani R.J. (2009). Statistical approaches in landscape genetics: an evaluation of methods for linking landscape and genetic data. *Ecography* 32: 818-830.

Banks S.C., Blyton M.D.J., Blair D., McBurney L. and Lindenmayer D.B. (2012). Adaptive responses and disruptive effects: how major wildfire influences kinship-based social interactions in a forest marsupial. *Molecular Ecology* 21: 673-684.

Banks S.C., Dujardin M., McBurney L., Blair D., Barker M. and Lindenmayer D.B. (2011). Starting points for small mammal population recovery after wildfire: recolonisation or residual populations? *Oikos* 120: 26-37.

Bates D., Maechler M. and Bolker B. (2011). *lme4: linear mixed-effects models using S4 classes.* R package, version 0.999375-40. http://lme4.r-forge.r-project.org/ (accessed September 2011).

Berry O., Tocher M.D., Gleeson D.M. and Sarre S.D. (2005). Effect of vegetation matrix on animal dispersal: genetic evidence from a study of endangered skinks. *Conservation Biology* 19: 855-864.

Berry O., Tocher M.D. and Sarre S.D. (2004). Can assignment tests measure dispersal? *Molecular Ecology* 13: 551-561.

Bradstock R.A., Bedward M., Gill A.M. and Cohn J.S. (2005). Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. *Wildlife Research* 32: 409-423.

Bradstock R.A. and Cohn J.S. (2002). Fire regimes and biodiversity in semi-arid mallee ecosystems. In: *Flammable Australia: the fire regimes and biodiversity of a continent.* (eds. Bradstock RA, Williams JE, Gill AM). Cambridge University Press, Cambridge.

Brockhurst M.A., Buckling A. and Gardner A. (2007). Cooperation peaks at intermediate disturbance. *Current Biology* 17: 761-765.

Butz R.J. (2009). Traditional fire management: historical fire regimes and land use change in pastoral East Africa. *International Journal of Wildland Fire* 18: 442-450.

Clarke M.F. (2008). Catering for the needs of fauna in fire management: science or just wishful thinking? *Wildlife Research* 35: 385-394.

Cohn J.S. (1995). The vegetation of Nombinnie and Round Hill Nature Reserves, central-western New South Wales. *Cunninghamia* 4: 81-101.

CSIRO (2011). *One-second SRTM digital elevation model.* Commonwealth Scientific and Industrial Research Organisation. http://www.csiro.au/science/One-second-SRTM-Digital-Elevation-Model.html.

Cushman S.A., McKelvey K.S., Flather C.H. and McGarigal K. (2008). Do forest community types provide a sufficient basis to evaluate biological diversity? *Frontiers in Ecology and the Environment* 6: 13-17.

Cushman S.A., McKelvey K.S., Hayden J. and Schwartz M.K. (2006). Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. *The American Naturalist* 168: 486-499.

DiBattista J.D., Feldheim K.A., Garant D., Gruber S.H. and Hendry A.P. (2011). Anthropogenic disturbance and evolutionary parameters: a lemon shark population experiencing habitat loss. *Evolutionary Applications* 4: 1-17.

Driscoll D.A. and Hardy C.M. (2005). Dispersal and phylogeography of the agamid lizard *Amphibolurus nobbi* in fragmented and continuous habitat. *Molecular Ecology* 14: 1613-1629.

Driscoll D.A. and Henderson M.K. (2008). How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model. *Biological Conservation* 141: 460-471.

Driscoll D.A., Lindenmayer D.B., Bennett A.F., Bode M., Bradstock R.A., Cary G.J., Clarke M.F., Dexter N., Fensham R., Friend G., Gill A.M., James S., Kay G., Keith D.A., MacGregor C., Russell-Smith J., Salt D., Watson J.E.M., Williams R.J. and York A. (2010). Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation* 143: 1928-1939.

Driscoll D.A., Smith A.L., Blight S.R. and Maindonald J. (2012). Reptile responses to fire and the risk of post-disturbance sampling bias. *Biodiversity and Conservation*: DOI 10.1007/s10531-10012-10267-10535.

Dubey S. and Shine R. (2010). Restricted dispersal and genetic diversity in populations of an endangered montane lizard (*Eulamprus leuraensis*, Scincidae). *Molecular Ecology* 19: 886-897.

Fox B.J. (1982). Fire and mammalian secondary succession in an Australian coastal heath. *Ecology* 63: 1332-1341.

Frankham R. (1996). Relationship of genetic variation to population size in wildlife. *Conservation Biology* 10: 1500-1508.

Frankham R. (1997). Do island populations have less genetic variation than mainland populations? *Heredity* 78: 311-327.

Franklin D.C., Petty A.M., Williamson G.J., Brook B.W. and Bowman D.M.J.S. (2008). Monitoring contrasting land management in the savanna landscapes of northern Australia. *Environmental Management* 2008.

Fuller S.J., Bull C.M., Murray K. and Spencer R.J. (2005). Clustering of related individuals in a population of the Australian lizard, *Egernia frerei*. *Molecular Ecology* 14: 1207-1213.

Funk W.C., Donnelly M.A. and Lips K.R. (2005). Alternative views of amphibian toe-clipping. *Nature* 433: 193.

Gardner M.G., Bull C.M., Cooper S.J.B. and Duffield G.A. (2001). Genetic evidence for a family structure in stable social aggregations of the Australian lizard *Egernia stokesii*. *Molecular Ecology* 10: 175-183.

Goslee S.C. and Urban D.L. (2007). The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software* 22: 1-19.

Griffiths A.D. (1999). Demography and home range of the frillneck lizard, *Chlamydosaurus kingii* (Agamidae), in northern Australia. *Copeia* 1999: 1089-1096.

Guillot G., Estoup A., Mortier F. and Cosson J.-F. (2005). A spatial statistical model for landscape genetics. *Genetics* 170: 1261-1280.

Hardy O.J. and Vekemans X. (2002). SPAGEDI: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Molecular Ecology Notes* 2: 618-620.

Haslem A., Kelly L.T., Nimmo D.G., Watson S.J., Kenny S.A., Taylor R.S., Avitabile S.C., Callister K.E., Spence-Bailey L.M., Clarke M.F. and Bennett A.F. (2011). Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. *Journal of Applied Ecology* 48: 247-256.

Hochberg Y. (1988). A sharper Bonferroni procedure for multiple tests of significance. *Biometrika* 75: 800-802.

Hoehn M., Sarre S. and Henle K. (2007). The tales of two geckos: does dispersal prevent extinction in recently fragmented populations? *Molecular Ecology* 16: 3299-3312.

Holland G.J. and Bennett A.F. (2011). Recolonization of forest fragments by a native rodent following experimental 'extinctions'. *Austral Ecology* 36: 521-529.

Hutchinson M.F. (2011). *ANUDEM Version 5.3* Fenner School of Environment and Society, ANU. http://fennerschool.anu.edu.au/research/publications/software-datasets/anudem.

Konvicka M., Zimmermann K., Klimova M., Hula V. and Fric Z. (2012). Inverse link between density and dispersal distance in butterflies: field evidence from six co-occurring species. *Population Ecology* 54: 91-101.

Landguth E.L., Cushman S.A., Schwartz M.K., McKelvey K.S., Murphy M. and Luikart G. (2010). Quantifying the lag time to detect barriers in landscape genetics. *Molecular Ecology* 19: 4179-4191.

Langlands P.R., Brennan K.E.C., Framenau V.W. and Main B.Y. (2011). Predicting the post-fire responses of animal assemblages: testing a trait-based approach using spiders. *Journal of Animal Ecology* 80: 558-568.

Leberg P.L. (2002). Estimating allelic richness: effects of sample size and bottlenecks. *Molecular Ecology* 11: 2445-2449.

Lee-Yaw J.A., Davidson A., McRae B.H. and Green D.M. (2009). Do landscape processes predict phylogeographic patterns in the wood frog? *Molecular Ecology* 18: 1863-1874.

Legendre P., Lapointe F.-J. and Casgrain P. (1994). Modeling brain evolution from behavior: a permutational regression approach. *Evolution* 48: 1487-1499.

Letnic M., Dickman C.R., Tischler M.K., Tamayo B. and Beh C.-L. (2004). The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *Journal of Arid Environments* 59: 85-114.

Levy E., Kennington W.J., Tomkins J.L. and LeBas N.R. (2010). Land clearing reduces gene flow in the granite outcrop-dwelling lizard, *Ctenophorus ornatus*. *Molecular Ecology* 19: 4192-4203.

Lindenmayer D.B., Wood J.T., MacGregor C., Michael D.R., Cunningham R.B., Crane M., Montague-Drake R., Brown D., Muntz R. and Driscoll D.A. (2008). How predictable are reptile responses to wildfire? *Oikos* 117: 1086-1097.

Lyet A., Cheylan M., Prodon R. and Besnard A. (2009). Prescribed fire and conservation of a threatened mountain grassland specialist: a capture-recapture study on the Orsini's viper in the French alps. *Animal Conservation* 12: 238-248.

Martins E.P. (1994). Phylogenetic perspectives on the evolution of lizard territoriality. In: *Lizard Ecology: Historical and Experimental Perspectives.* (eds. Vitt LJ, Pianka ER), pp. 117-144. Princeton University Press, Princeton, N.J.

Mazerolle M.J. (2011). *AICcmodavg.* R package, version 1.2. http://cran.r-project.org/web/packages/AICcmodavg/index.html (accessed September 2011).

McRae B.H. and Beier P. (2007). Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Science USA* 104: 19885-19890.

Moreira F., Viedma O., Arianoutsou M., Curt T., Koutsias N., Rigolot E., Barbati A., Corona P., Vaz P., Xanthopoulos G., Mouillot F. and Bilgili E. (2011). Landscape-wildfire interactions in southern Europe: implications for landscape management. *Journal of Environmental Management* 92: 2389-2402.

Murphy M.A., Evans J.S. and Storfer A. (2010). Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. *Ecology* 91: 252-261.

Parr C.L. and Andersen A.N. (2006). Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Conservation Biology* 20: 1610-1619.

Pausas J.G. and Lloret F. (2007). Spatial and temporal patterns of plant functional types under simulated fire regimes. *International Journal of Wildland Fire* 16: 484-492.

Peakall R. and Lindenmayer D.B. (2006). Genetic insights into population recovery following experimental perturbation in a fragmented landscape. *Biological Conservation* 132: 520-532.

Peters R.A. and Ord T.J. (2003). Display response of the Jacky Dragon, *Amphibolurus muricatus* (Lacertilia: Agamidae), to intruders: a semi-Markovian process. *Austral Ecology* 28: 499-506.

Pianka E.R. (1969a). Habitat specificity, speciation, and species density in Australian desert lizards. *Ecology* 50: 498-502.

Pianka E.R. (1969b). Sympatry of desert lizards (*Ctenotus*) in Western Australia. *Ecology* 50: 1012-1030.

Pianka E.R. (1972). Zoogeography and speciation of Australian desert lizards: an ecological perspective. *Copeia* 1972: 127-145.

Pianka E.R. and Pianka H.D. (1976). Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australian desert. *Copeia* 1976: 125-142.

Porter A.H. (1999). Refugees from lost habitat and reorganization of genetic population structure. *Conservation Biology* 13: 850-859.

Prevedello J.A., Forero-Medina G. and Vieira M.V. (2010). Movement behaviour within and beyond perceptual ranges in three small mammals: effects of matrix type and body mass. *Journal of Animal Ecology* 79: 1315-1323.

Pritchard J.K., Stephens M. and Donnelly P. (2000). Inference of population structure using multilocus genotype data. *Genetics* 155: 945-959.

R Development Core Team (2011). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Raymond M. and Rousset F. (1995). GENEPOP (Version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity* 86: 248-249.

Robinet C., Lance D.R., Thorpe K.W., Onufrieva K.S., Tobin P.C. and Liebhold A.M. (2008). Dispersion in time and space affect mating success and Allee effects in invading gypsy moth populations. *Journal of Animal Ecology* 77: 966-973.

Robinson A.C. and Heard M.B. (1985). National Parks. In: *Natural history of Eyre Peninsula.* (eds. Twidale CR, Tyler MJ, Davies M). Royal Society of South Australia, Adelaide, SA.

Rousset F. (2000). Genetic differentiation between individuals. *Journal of Evolutionary Biology* 13: 58-62.

Sanz-Aguilar A., Anadón J.D., Giménez A., Ballestar R., Graciá E. and Oro D. (2011). Coexisting with fire: the case of the terrestrial tortoise *Testudo graeca* in mediterranean shrublands. *Biological Conservation* 144: 1040-1049.

Schmuki C., Vorburger C., Runciman D., Maceachern S. and Sunnucks P. (2006). When log-dwellers meet loggers: impacts of forest fragmentation on two endemic log-dwelling beetles in southeastern Australia. *Molecular Ecology* 15: 1481-1492.

Schrey A.W., Fox A.M., Mushinsky H.R. and McCoy E.D. (2011). Fire increases variance in genetic characteristics of Florida Sand Skink (*Plestiodon reynoldsi*) local populations. *Molecular Ecology* 20: 56-66.

Schtickzelle N., Joiris A., Van Dyck H. and Baguette M. (2007). Quantitative analysis of changes in movement behaviour within and outside habitat in a specialist butterfly. *BMC Evolutionary Biology* 7: 4.

Shanahan D.F., Possingham H.P. and Riginos C. (2011). Models based on individual level movement predict spatial patterns of genetic relatedness for two Australian forest birds. *Landscape Ecology* 26: 137-148.

Short Bull R.A., Cushman S.A., Mace R., Chilton T., Kendall K.C., Landguth E.L., Schwartz M.K., McKelvey K., Allendorf F.W. and Luikart G. (2011). Why replication is important in landscape genetics: American black bear in the Rocky Mountains. *Molecular Ecology* 20: 1092-1107.

Smith A.L., Bull C.M. and Driscoll D.A. (2012). Post-fire succession affects abundance and survival but not detectability in a knob-tailed gecko. *Biological Conservation* 145: 139-147.

Smith A.L., Bull C.M. and Driscoll D.A. (Chapter 3). A six-year study reveals previously undetected responses to fire in reptiles. In: *Reptile dispersal and demographics after fire: process-based knowledge to assist fire management for biodiversity*. Submitted PhD thesis, The Australian National University.

Smith A.L., Gardner M.G., Bull C.M. and Driscoll D.A. (2011). Primers for novel microsatellite markers in "fire-specialist" lizards (*Amphibolurus norrisi, Ctenotus atlas* and *Nephrurus stellatus*) and their performance across multiple populations. *Conservation Genetics Resources* 3: 345-350.

Smith A.L., Gardner M.G., Bull C.M. and Fenner A.L. (2009). Restricted gene flow in the endangered pygmy bluetongue lizard (*Tiliqua adelaidensis*) in a fragmented agricultural landscape. *Wildlife Research* 36: 466-478.

Smith L.M. and Burgoyne L.A. (2004). Collecting, archiving and processing DNA from wildlife samples using FTA(R) databasing paper. *BMC Ecology* 4: http://www.biomedcentral.com/1472-6785/1474/1474.

South S.L. (2010). *Natural history and spatial ecology of Amphibolurus norrisi in southern Australia.* Unpublished honours thesis, Flinders University, Adelaide.

Spear S.F. and Storfer A. (2010). Anthropogenic and natural disturbance lead to differing patterns of gene flow in the Rocky Mountain tailed frog, *Ascaphus montanus*. *Biological Conservation* 143: 778-786.

Specht R.L. (1972). *The Vegetation of South Australia.* AB James, Government Printer, Adelaide, SA.

Stephens P.A., Sutherland W.J. and Freckleton R.P. (1999). What is the Allee effect? *Oikos* 87: 185-190.

Storfer A., Murphy M.A., Spear S.F., Holderegger R. and Waits L.P. (2010). Landscape genetics: where are we now? *Molecular Ecology* 19: 3496-3514.

Stow A.J. and Sunnucks P. (2004). High mate and site fidelity in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. *Molecular Ecology* 13: 419-430.

Stow A.J., Sunnucks P., Briscoe D.A. and Gardner M.G. (2001). The impact of habitat fragmentation on dispersal in Cunningham's skink (*Egernia cunninghami*): evidence from allelic and genotypic analyses of microsatellites. *Molecular Ecology* 10: 867-878.

Sumner J., Jessop T., Paetkau D. and Moritz C. (2004). Limited effect of anthropogenic habitat fragmentation on molecular diversity in a rain forest skink, *Gnypetoscincus queenslandiae*. *Molecular Ecology* 13: 259-269.

Sumner J., Rousset F., Estoup A. and Moritz C. (2001). 'Neighbourhood' size, dispersal and density estimates in the prickly forest skink (*Gnypetoscincus queenslandiae*) using individual genetic and demographic methods. *Molecular Ecology* 10: 1917-1927.

Sutton J.T., Nakagawa S., Robertson B.C. and Jamieson I.G. (2011). Disentangling the roles of natural selection and genetic drift in shaping variation at MHC immunity genes. *Molecular Ecology* 20: 4408-4420.

Templeton A.R., Brazeal H. and Neuwald J.L. (2011). The transition from isolated patches to a metapopulation in the eastern collared lizard in response to prescribed fires. *Ecology* 92: 1736-1747.

Templeton A.R., Robertson R.J., Brisson J. and Strasburg J. (2001). Disrupting evolutionary processes: the effect of habitat fragmentation on collared lizards in the

Missouri Ozarks. *Proceedings of the National Academy of Science, USA.* 98: 5426-5432.

Twidale C.R. and Campbell E.M. (1985). The form of the land surface. In: *Natural history of Eyre Peninsula.* (eds. Twidale CR, Tyler MJ, Davies M). Royal Society of South Australia, Adelaide, SA.

van Nouhuys S. and Hanski I. (2002). Colonization rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape. *Journal of Animal Ecology* 71: 639-650.

Vilà-Cabrera A., Saura-Mas S. and Lloret F. (2008). Effects of fire frequency on species composition in a Mediterranean shrubland. *Écoscience* 15: 519-528.

Waichman A.V. (1992). An alphanumeric code for toe clipping amphibians and reptiles. *Herpetological Review* 23: 19-21.

Walker F.M., Sunnucks P. and Taylor A.C. (2008). Evidence for habitat fragmentation altering within-population processes in wombats. *Molecular Ecology* 17: 1674-1684.

Welsh A.H. (1996). *Aspects of Statistical Inference* John Wiley & Sons, Inc., New York.

Westgate M.J., Driscoll D.A. and Lindenmayer D.B. (2012). Can the intermediate disturbance hypothesis and information on species traits predict anuran responses to fire? *Oikos*: DOI 10.1111/j.1600-0706.2011.19863.x.

Williams J.R., Driscoll D.A. and Bull C.M. (2011). Roadside connectivity does not increase reptile abundance or richness in a fragmented mallee landscape. *Austral Ecology*.

Wilson S. and Swan G. (2010). *A Complete Guide to Reptiles of Australia*, 3 edn. New Holland, Sydney.

Wright S. (1943). Isolation by distance. *Genetics* 28: 114-138.

Zuur A.F., Ieno E.N., Walker N.J., Saveliev A.A. and Smith G.M. (2009). *Mixed effects models and extensions in ecology with R.* Springer, New York.

7.8 Supporting material

7.8.1 Site information

Table S7.1 Sites where DNA samples from *Amphibolurus norrisi* and *Ctenotus atlas* were collected on the Eyre Peninsula, South Australia. Samples were collected over six field seasons (Season one was Dec 2004 – Feb 2005 and season six was Nov 2009 – Feb 2010).

Reserve	**Site**	**Last fire**	**N *A. norrisi***	**N *C. atlas***	**Seasons DNA collected**	**Collection method**
Heggaton	N1	1997	1	9	2-4	Transect
	N2	1997	1	0	4	Transect
	N3	1960	10	8	1-4	Transect
	N4	1960/2006	2/0	7/12	1-4	Transect
	S1	2001	1	1	1-2	Transect
	S2	2001	2	0	3-4	Transect
	S3	1960	18	4	1-4	Transect
	S4	1960	6	2	1-2	Transect
Hincks	I1	1999	1	0	4	Transect
	I3	1977/2006	5/2	9/8	1-4	Transect
	I4	1977/2006	2/3	13/16	1-3	Transect
	HI1	1966	2	15	4-5	Grid
	HI2	1966	7	23	4-6	Grid
	HI3	1966	11	25	4-6	Grid
	HI4	1966	5	29	4-6	Grid
	HI5	1966	17	17	4-6	Grid
	HI6	1966	11	26	4-6	Grid
	HI7	1966	13	34	4-6	Grid
	HIE1	2006	0	6	5	Grid
	HIE2	2006	8	6	5-6	Grid
	HIM1	1999	24	12	5-6	Grid
	HIM2	1999	11	2	5-6	Grid
	66TK	1966	1	0	6	Manual
	MTK	1999	3	0	6	Manual
	06TK	2006	1	0	6	Manual
Munyaroo	M1	1990	3	1	1-2	Transect
	M2	1990	0	7	1-2	Transect
	M3	1960	6	0	1-2	Transect
	M4	1960	0	8	2	Transect
Pinkawillinie	P3	1986/2005	-	9/6	1-4	Transect
	P4	1986/2005	-	5/7	1-4	Transect
	P8	1986	-	14	3-4	Transect
	PL1	1960	-	6	5-6	Grid
	PL2	1960	-	2	5-6	Grid
	PL3	1960	-	10	5-6	Grid
	PL4	1960	-	14	5-6	Grid
	PM1	2001	-	1	6	Grid
	PM2	2001	-	3	6	Grid
TOTAL			177	377		

7.8.2 Abundance estimates for Heggaton and Munyaroo

Reptile abundance does not always respond linearly to time since fire (Smith et al. Chapter 3) and population density can affect dispersal (Stephens et al. 1999; Robinet et al. 2008). We therefore investigated models of landscape resistance based on the abundance of *Amphibolurus norrisi* and *Ctenotus atlas* at different times since fire (TSF). Regional variation in responses to TSF has been previously observed for both species (Driscoll & Henderson 2008; Driscoll et al. 2012) so we needed accurate estimates of abundance from each location to parameterise our landscape resistance models. Smith et al. (Chapter 3) developed models to predict the effect of TSF on abundance of both species at Hincks and Pinkawillinie but no estimates were available for Heggaton and Munyaroo. We therefore produced abundance estimates for these locations to use in our landscape resistance analysis.

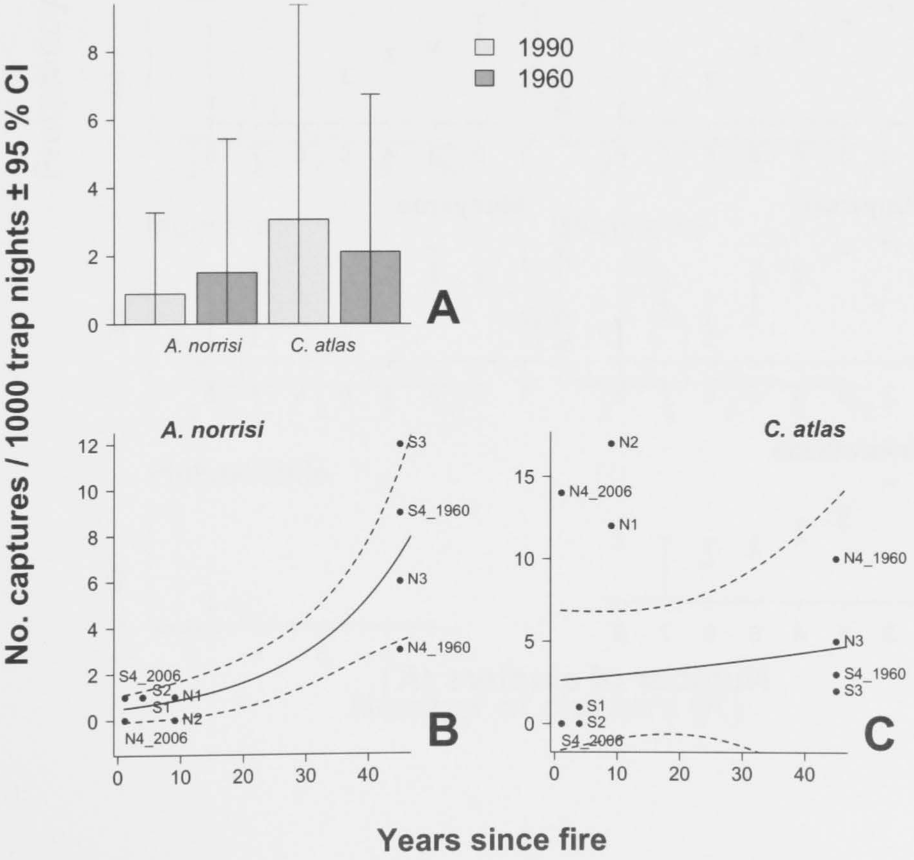
We combined four years of pitfall trapping data to estimate the effect of TSF on *A. norrisi* and *C. atlas*. The first two years of data were presented by Driscoll and Henderson (2008) and the subsequent two years by Driscoll et al. (2012). Data from Munyaroo were only available from the first two years. We treated sites that burnt during the study as separate observations before and after fire because reptile community composition (Driscoll & Henderson 2008) and habitat structure (Smith et al. 2012) at our sites are influenced more by fire history than geographic proximity within reserves. All data were pooled for each site observation, and capture rates were standardised by trap effort. We analysed each species at each location separately using generalised linear mixed models and fitted a random term to account for potential dependence among sites within the same fire boundary. Full details of the analytical method are described by Smith et al. (Chapter 3). There were only two times since fire at Munyaroo and we did not need to parameterise areas where we had not sampled so we used a categorical predictor variable. Numerical predictors were used for Heggaton.

For Munyaroo, dispersion parameters were 12.0 for *A. norrisi* and 16.4 for *C. atlas*, so we fitted an observation level random effect to account for overdispersion. There was evidence of underdispersion at Heggaton (dispersion parameter = 0.64 for *A. norrisi* and 0.63 for *C. atlas*). There was no effect of TSF on abundance for either species at Munyaroo, or for *C. atlas* at Heggaton (Table S7.2, Fig. S7.1a,c). Abundance in *A. norrisi* at Heggaton significantly increased with TSF (Table S7.2, Fig. S7.1b).

Table S7.2 Results from generalised linear mixed models to investigate the effect of fire on the number of captures in *Amphibolurus norrisi* and *Ctenotus atlas*. The significant result is shown in bold.

Species	Reserve	Parameter	Estimate	SE	z-value	P-value
A. norrisi	Munyaroo	Intercept	0.417	1.323	0.315	0.753
		Fire category	-0.537	1.909	-0.281	0.779
	Heggaton	Intercept	-0.717	0.593	-1.209	0.227
		Time since fire	**0.060**	**0.015**	**4.037**	**< 0.001**
C. atlas	Munyaroo	Intercept	0.759	1.106	0.686	0.493
		Fire category	0.368	1.523	0.241	0.809
	Heggaton	Intercept	0.955	0.840	1.136	0.256
		Time since fire	0.013	0.031	0.416	0.677

Fig. S7.1 The effect of fire on capture rates in *Amphibolurus norrisi* and *Ctenotus atlas* at Munyaroo (A) and Heggaton (B and C).



7.8.3 Genetic structure analysis

Fig. S7.2 We did not detect any genetic structure in *Amphibolurus norrisi* or *Ctenotus atlas* using STRUCTURE. A single genetic cluster was most likely in each reserve, and in the overall sample for both species.

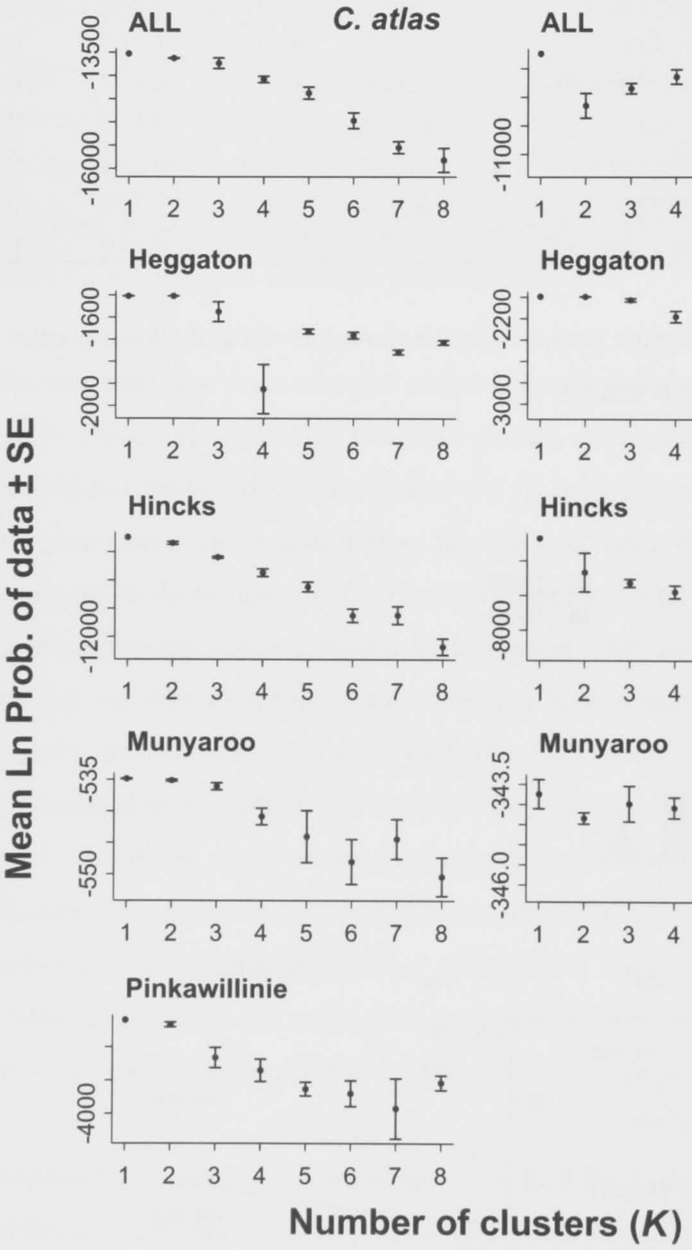


Fig. S7.3 We detected some genetic structure in the samples from *Amphibolurus norrisi* and *Ctenotus atlas* using GENELAND. The mode indicates the most likely number of clusters in each data set. Assignment probabilities for the overall sample in *C. atlas* and for *A. norrisi* at Heggaton are shown in the Results (Fig. 7.2). Genetic structure identified in the samples from *C. atlas* at Heggaton and both species at Munyaroo were likely spurious (see Fig. S7.4 below).

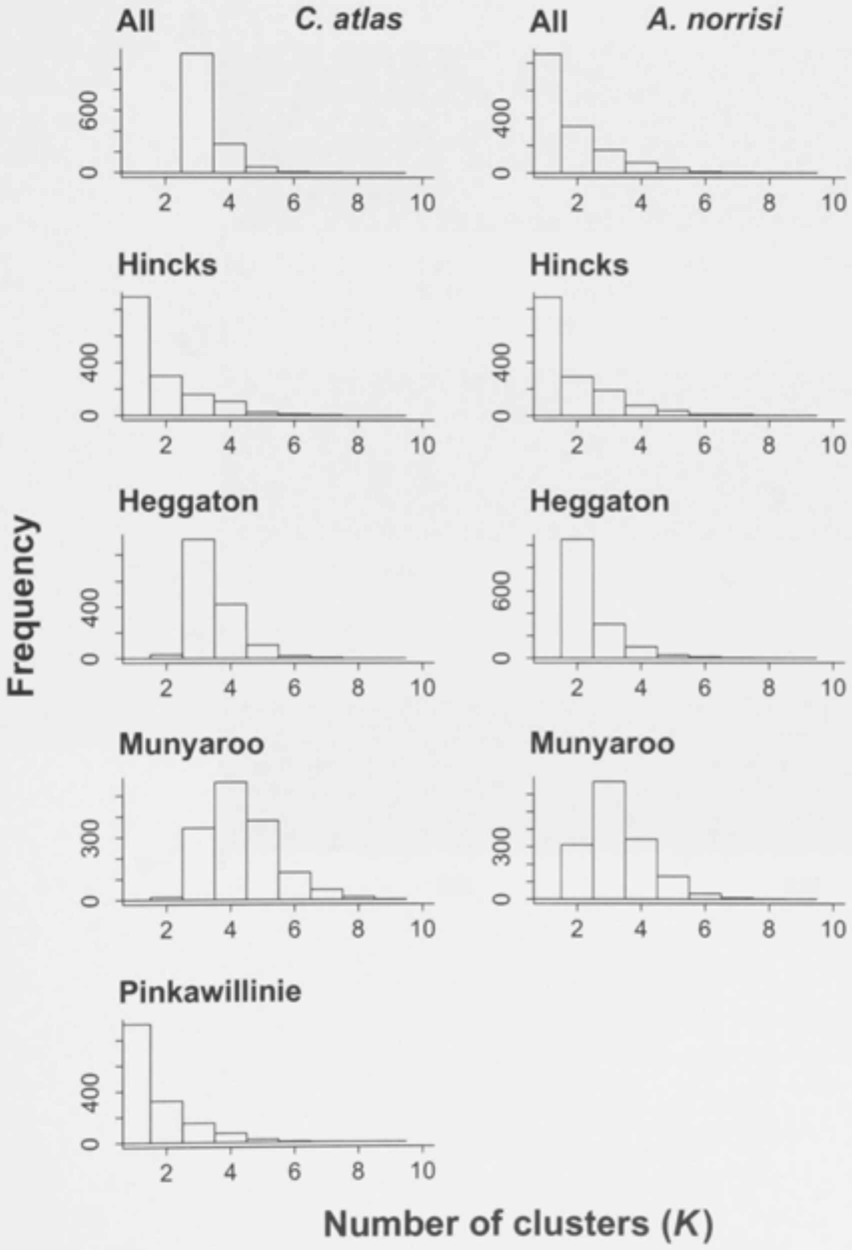
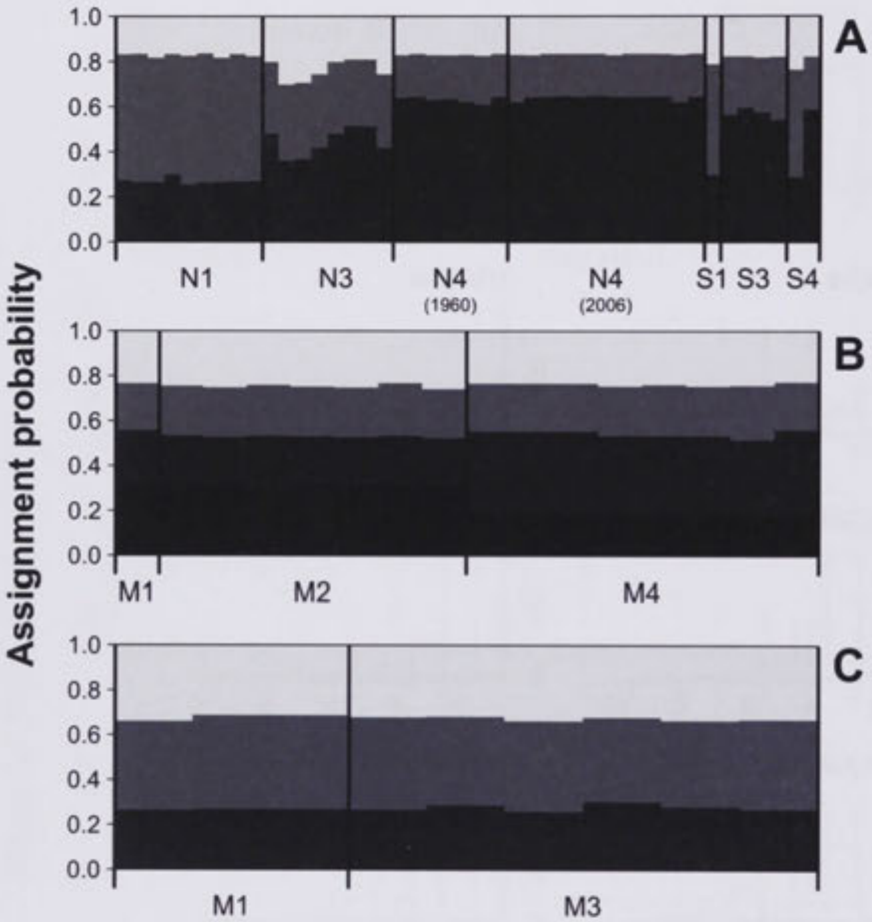


Fig. S7.4 Probabilities of assignment to genetic clusters (each bar represents an individual lizard) identified by GENELAND. In the samples from *Ctenotus atlas*, three genetic clusters at were identified at Heggaton (A) and four at Munyaroo (B). For *Amphibolurus norrisi* two genetic clusters were identified at Munyaroo (C). However, these results were not reliable as individuals were given an approximately equal probability to each cluster.



7.8.4 Landscape resistance in Ctenotus atlas

Table S7.3 None of the models of landscape resistance that we tested for *Ctenotus atlas* explained significant variation in gene flow.

Model	**Relationship**	R^2	*P*-value
HINCKS (N = 219)			
Isolation by distance	+	0.0001	0.900
Elevation	+	0.0001	0.907
Time since fire	+	0.0001	0.786
Abundance	-	0.0003	0.647
Fire frequency	-	0.0004	0.568
HEGGATON (Before 2006 fires, N = 21)			
Isolation by distance	-	0.0014	0.638
Elevation	-	0.0024	0.543
Time since fire	+	0.0001	0.918
HEGGATON (After 2006 fires, N = 22)			
Isolation by distance	+	0.0009	0.770
Elevation	+	0.0007	0.805
Time since fire	+	0.0116	0.485
MUNYAROO (N = 16)			
Isolation by distance	+	0.0108	0.315
Elevation	+	0.0101	0.347
Time since fire	+	0.0054	0.472
PINKAWILLINIE (N = 63)			
Isolation by distance	+	0.0010	0.223
Elevation	+	0.0011	0.207
Time since fire	-	0.0042	0.316
Abundance	-	0.0055	0.253

7.8.5 Fire and reserve effects on allelic richness (AR)

Fig. S7.5 There were significant effects of TSF on AR in *Amphibolurus norrisi* when sample sizes (N) of five to ten were used as a standardisation. When N = 5 and N = 6 there were additive effects of reserve on AR, with Munyaroo (orange) having lower AR than Hincks (blue) and Heggaton (red). Model estimates and 95 % confidence intervals are shown over the raw data.

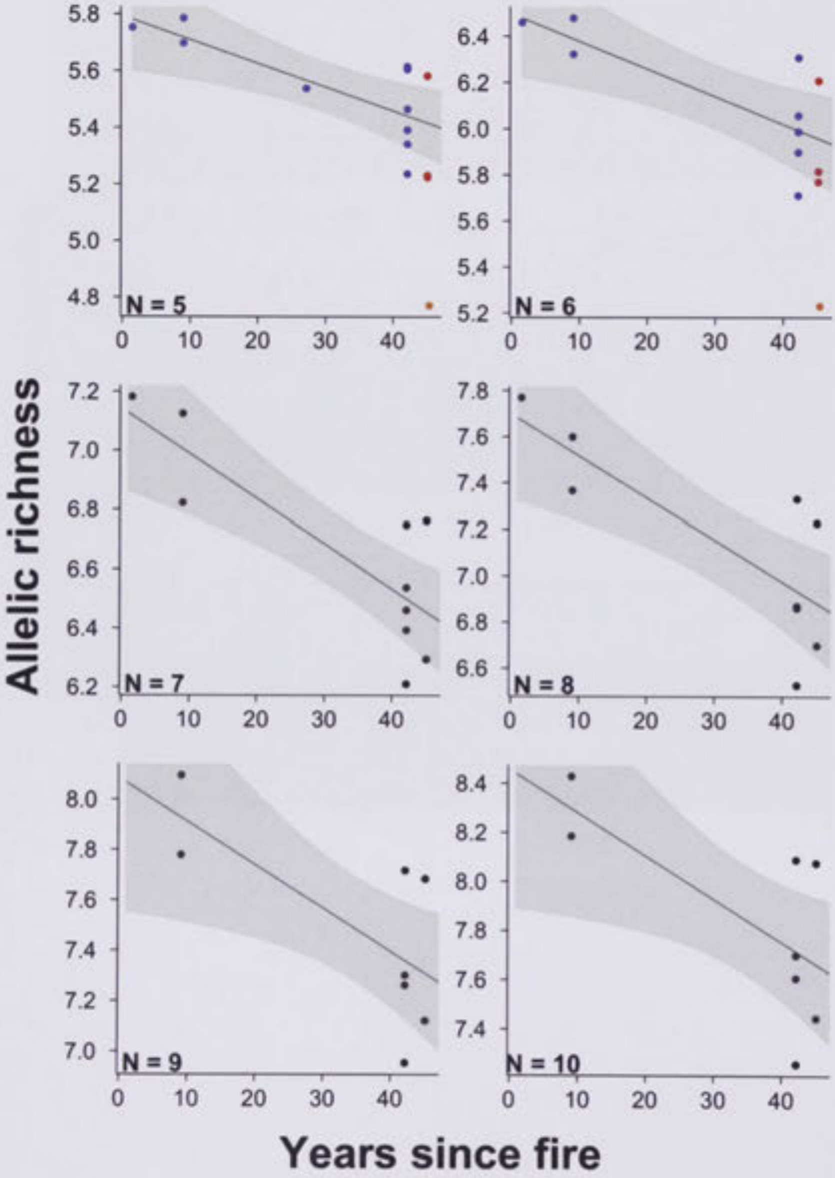
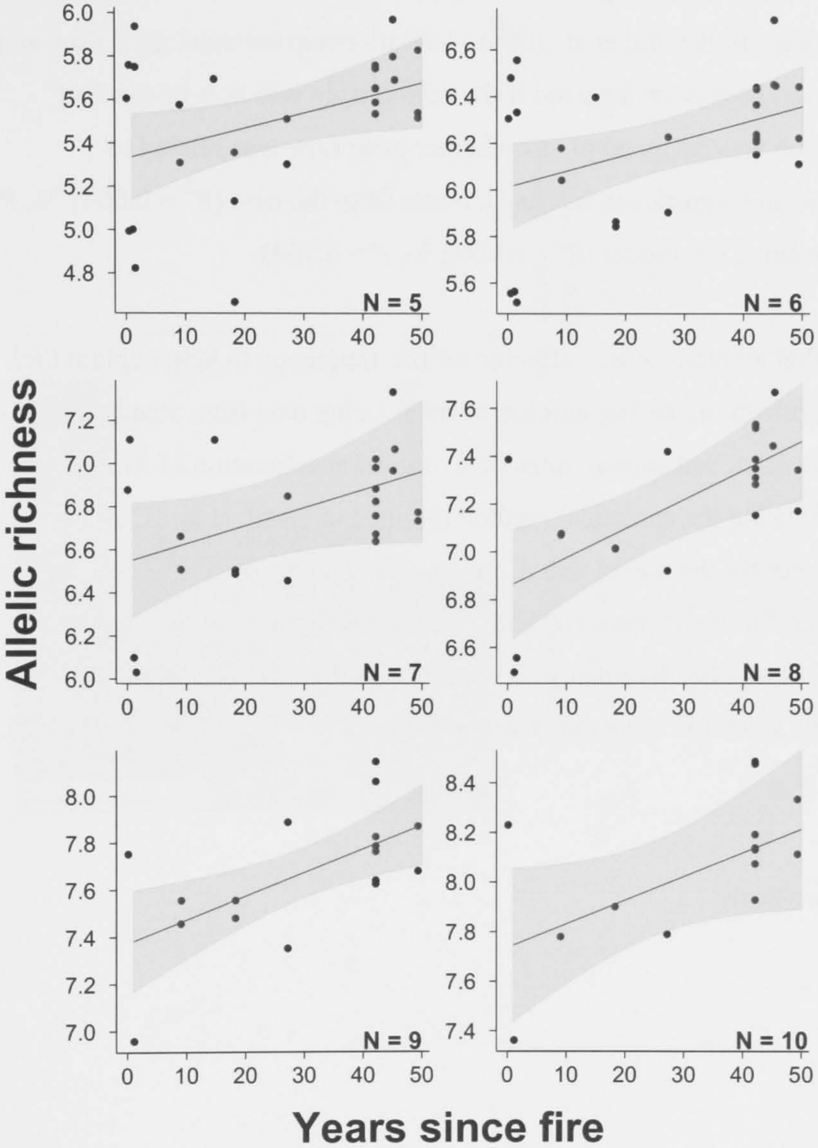


Fig. S7.6 There were significant relationships between TSF on AR in *Ctenotus atlas* except when N = 7 (P = 0.087) and N = 10 (P = 0.69) were used as standardisations. There were no interactive or additive effects of reserve on AR.

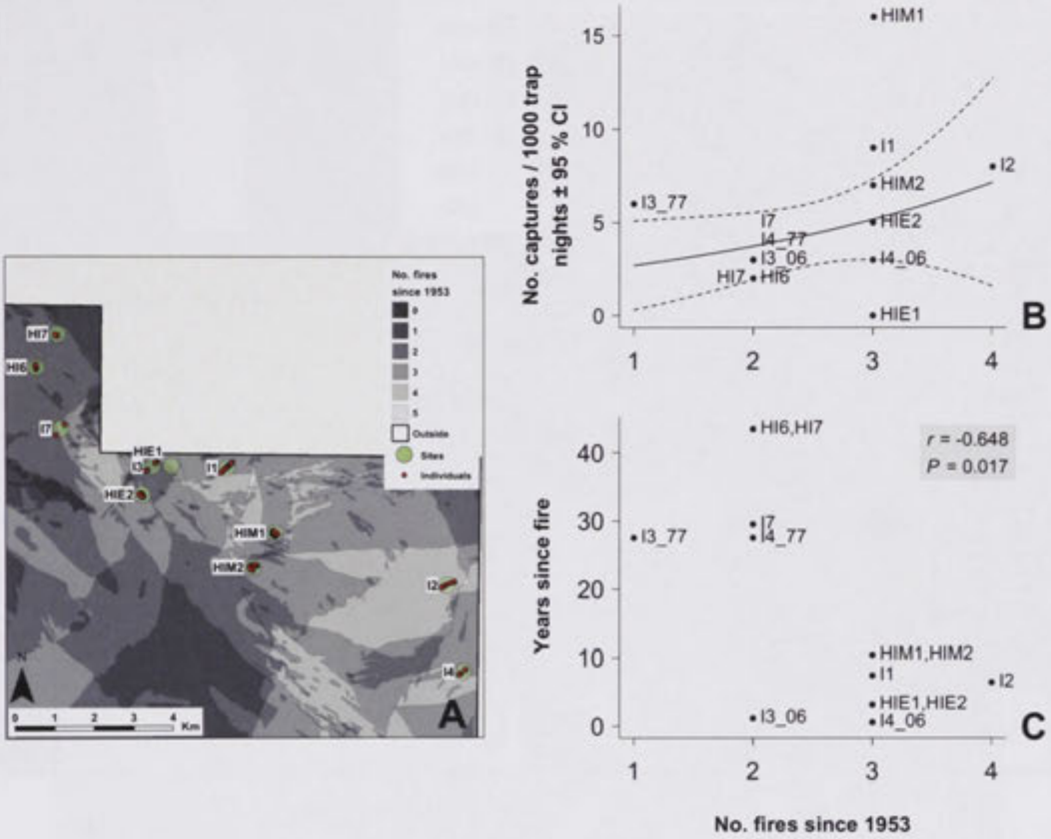


7.8.6 Effect of fire frequency on Amphibolurus norrisi

In previous studies we modelled the abundance of *A. norrisi* using the quadratic term of time since fire (Smith et al. Chapter 3). We were unable to examine gene flow using a quadratic model because the matrix regression method we used relies on linearity between the two matrices (Balkenhol et al. 2009). A relationship between gene flow and time since fire would not have been detected if the relationship was non-linear. Our abundance model, which was designed to test whether gene flow was related to population density, was not significant, but had a better fit to the data ($R^2 = 0.0047$ %, $P = 0.090$) than the time since fire model ($R^2 = 0.0002$ %, $P = 0.764$).

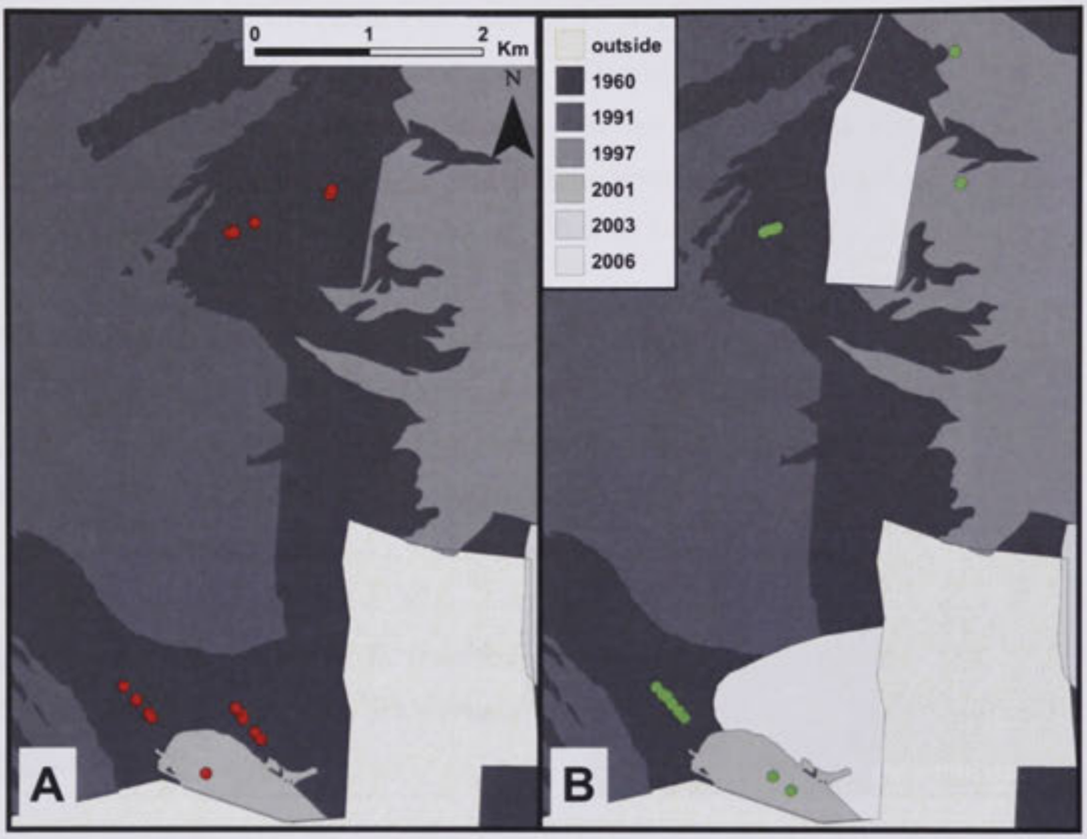
We investigated whether abundance was affected by fire frequency to help explain the decline in gene flow with an increasing number of fires. Using data from standardised pitfall trap surveys, we modelled capture rates of *A. norrisi* as a function of fire frequency (Fig. S7.7a) using the analytical method outlined in Smith et al. (Chapter 3). The dispersion parameter for the model was 3.2 so we fitted an observation level random term to account for overdispersion. There was a non-significant increase in capture rates with increasing fire frequency ($P = 0.197$, Fig. S7.7b). We also found that fire frequency and time since fire were negatively correlated ($r = -0.648$, $P = 0.017$, Fig. S7.7c).

Fig. S7.7 Capture rates of *Amphibolurus norrisi* were recorded during pitfall trap surveys at Hincks from sites spanning a range of fire frequencies (A). There was a positive (but non-significant) relationship between capture rates and fire frequency (B). Fire frequency at Hincks is correlated with time since fire (C).



7.8.7 Amphibolurus norrisi *samples at Heggaton*

Fig. S7.8 The location of 20 *A. norrisi* individuals sampled at Heggaton prior to prescribed fires in April 2006 (A), and 21 individuals sampled after the fires (B).



Chapter 8

Directions for fire management and future research

Conclusions

Mallee is home to a diverse ecological community. I recorded 17 reptile species in one hectare at this area in Pinkawillinie Conservation Park that last burnt in 1960 (Photo A.L. Smith, taken Dec 2009 at the site "PL4").

8.1 Process-based knowledge for fire management

Inappropriate fire management threatens the persistence of animal species in many ecosystems around the world (Lyet et al. 2009; Betts et al. 2010; Gregory et al. 2010; Templeton et al. 2011). Conducting fire management at scales that will allow animal species to persist in a landscape can be assisted by conceptual and simulation based fire-response models of species and ecological communities (Letnic et al. 2004; Bradstock et al. 2005; Driscoll et al. 2010). Such models rely on understanding the processes behind species responses to fire (Whelan et al. 2002; Clarke 2008; Driscoll et al. 2010). I aimed to determine which demographic and dispersal attributes of reptiles were important in influencing their response to fire regimes. The findings of my thesis are summarised in the following list (8.1.1), and the next section (8.2) explains the implications of these results for fire management.

8.1.1 Summary of results from my thesis:

1. Long-term and/or intensively sampled surveys are needed to detect fire responses in reptiles (Chapter 2).
2. Many mallee reptiles specialise on a particular successional stage, and there are contrasting responses to fire among the reptile community (Chapter 2).
3. Nocturnal burrowing reptiles may be early-successional while diurnal leaf-litter dwellers may be late-successional (Chapters 2 and 3), but trait-based models of succession in reptiles currently have limited predictive power.
4. Variation in post-fire survival and reproductive rates in *Nephrurus stellatus* may underlie their strong early-successional population response to fire (Chapter 4).
5. High levels of gene flow in *Ctenotus atlas*, *Nephrurus stellatus* and *Amphibolurus norrisi*, characterised using techniques developed in Chapter 5, suggest these species can maintain population connectivity across patchy fire mosaics (Chapters 6 and 7).
6. Dispersal in *Nephrurus stellatus* declines with increasing time since fire which may result from, or contribute to its decline in population density (Chapter 6).
7. Gene flow in *Amphibolurus norrisi* tends to increase after fire possibly because of a disruption of stable territory or social structure (Chapter 7).
8. Genetic diversity varies across fire mosaics in *Ctenotus atlas*, *Nephrurus stellatus* and *Amphibolurus norrisi* (Chapters 6 and 7).

My analysis of the mallee reptile community revealed that short-term studies can fail to detect important fire response patterns in mallee reptiles. I found many contrasting responses to fire among the reptile community that trait-based models of succession could not describe reliably. These findings have direct applications for fire management which are discussed in the next section (8.2).

The applicability of my species-level studies are less direct because fire management protocols must cater for a broad range of species within an ecosystem (Keith et al. 2002). The strength of the species-level results is that they give new insights into the processes behind fire responses in reptiles and will greatly contribute to the development of fire-response models for animal communities in future (discussed further in section 8.3). For example, Bradstock et al. (2005) used data on population density, reproduction and dispersal to parameterise a simulation model for the malleefowl, a bird that requires long-unburnt mallee for roosting and shelter. The results from my research will allow similar modelling projects to be conducted for reptiles. We now know that dispersal in *N. stellatus* and *A. norrisi* is likely to be affected by fire mosaics, while *C. atlas* probably has a similar dispersal rate across different post-fire stages. I also documented successional changes in survival and reproduction in *N. stellatus* – essential knowledge to accurately parameterise simulation models. My research therefore provides a foundation for quantifying extinction risk of fire specialist reptile species under different fire regime (Bradstock et al. 2005) and climate scenarios (Lawson et al. 2010).

8.2 Guidelines for fire management

My analysis of a six-year data set from the mallee reptile community identified many species with responses to fire that were not detected in previous analyses of data from shorter sampling periods (Chapter 2). It is important that short-term fire studies of vertebrates are interpreted with the knowledge that many responses to fire may not have been detected. It is often suggested that reptiles will benefit from fire (e.g. Bury 2004) but I found some evidence that late-successional responses to fire may be under represented in surveys of reptile communities. The needs of animals will vary among ecosystems, but late-successional habitats are likely to be very important for a suite of reptile species. These may be the same species that are difficult to detect because of their association with dense habitat features. There are many different responses to fire among the reptile community, so extreme fire regimes, including complete fire suppression and widespread burning, should be avoided.

My studies of the three target species suggest that dispersal, at the spatial scales I examined, may be sufficiently high to maintain gene flow when frequent fire maintains patchy habitat mosaics. The finding that fire mosaics can influence dispersal and genetic diversity in lizards emphasises once more the need to avoid extreme fire management regimes. The results of my thesis can be synthesised into three broad guidelines for fire management (8.2.1).

8.2.1 Management guidelines for reptile conservation:

1. Complete fire suppression and widespread prescribed burning should be avoided so that fire specialist species do not decline. This means that:
2. Fires that are small, relative to the area of habitat in question, should be used to prevent widespread wildfire from burning an entire reserve or patch of vegetation, and the focus should be on areas that do not have a natural fire mosaic.
3. Prescribed burning is probably not necessary in areas that have a complex natural fire mosaic (e.g. Hincks Wilderness Area), as connectivity among reptile populations appears high and the mosaic provides natural fire breaks.

The three target lizard species I studied are common on the Eyre Peninsula, but their strong population responses to fire meant that collecting sufficient data in their sub-optimal habitat was difficult. Data from the successional stages where the species are rare give us the best insights into why they decline, but these areas are the hardest to obtain information from. In addition, I had data from 44 reptile species overall, but less than half of these species had sufficient captures to conduct statistical analysis of population response to fire. Collecting data on rare species, or those that are not commonly detected using conventional survey methods, is a common problem in ecology (Manley et al. 2004; MacKenzie et al. 2005) and these challenges emphasise the importance of a precautionary approach to fire management (Keith et al. 2002).

8.3 Directions for future research

My thesis has advanced our understanding of the processes behind animal responses to fire. In particular, we now know that post-fire succession can drive variation in survival, reproduction and dispersal of fire specialist reptiles. This information can be used to build fire response models that quantify extinction risk of species under different fire regimes (e.g. Bradstock et al. 2005). My thesis has also raised a number of important questions that need to be tackled in future studies, and these are summarised below.

8.3.1 Important areas for future research

1. Determine demographic and dispersal processes behind fire responses in a greater range of vertebrate and invertebrate species (such studies are currently being conducted by my colleagues on birds in mallee ecosystems).
2. Improve our understanding of animal ecology so that trait-based models of succession have a better chance of predicting fire responses in animals (e.g. Langlands et al. 2011). This would require intensive field studies to document ecological needs of a wide range of species.
3. Use direct observations (e.g. Koch and Hero 2007) and occupancy research methods (e.g. Driscoll et al. 2012) to improve our understanding of fire responses in rare species, and in common species in sub-optimal successional stages.
4. Continue to apply genetic methods to examine modes of animal recolonisation after fire (e.g. Peakall and Lindenmayer 2006)
5. Examine demography and dispersal of fire specialists in small habitat fragments, where reptiles have additional pressures such as degraded vegetation and increased predation (e.g. Driscoll et al. 2012).
6. Undertake studies of animals in landscapes where the effects of fire frequency can be separated from effects of time since fire (e.g. Westgate et al. 2012).
7. Determine how the fire response of animals varies under different grazing regimes (e.g. Kirkpatrick et al. 2011) and climate change scenarios (e.g. Lawson et al. 2010)
8. Use spatially explicit simulation models to quantify appropriate spatial and temporal scales for prescribed burning (e.g. Bradstock et al. 2005) based on our new knowledge about how fire affects dispersal and demography in reptiles.

Among this list of future directions, the priority areas are determining how species are affected by different spatial scales (size and shape) and frequency of fire (Driscoll et al. 2010). This is particularly important in heavily fragmented landscapes where negative effects of fire regimes on animal species might interact with other pressures such as habitat degradation and predation (Driscoll et al. 2010) and where fires have the potential to burn entire habitat remnants (Gill & Allan 2008). Such studies are urgently needed to provide practical advice to management agencies in charge of managing fire for biodiversity. Although there is still much to be learnt, my thesis has demonstrated that knowledge of demographic and dispersal attributes can shed light on the processes behind fire responses in reptiles. Expanding on this research in the future will continue to assist fire management for biodiversity conservation.

8.4 References

Betts M.G., Hagar J.C., Rivers J.W., Alexander J.D., McGarigal K. and McComb B.C. (2010). Thresholds in forest bird occurrence as a function of the amount of early-seral broadleaf forest at landscape scales. *Ecological Applications* 20: 2116-2130.

Bradstock R.A., Bedward M., Gill A.M. and Cohn J.S. (2005). Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. *Wildlife Research* 32: 409-423.

Bury R.B. (2004). Wildfire, fuel reduction, and herpetofaunas across diverse landscape mosaics in northwestern forests. *Conservation Biology* 18: 968-975.

Clarke M.F. (2008). Catering for the needs of fauna in fire management: science or just wishful thinking? *Wildlife Research* 35: 385-394.

Driscoll D.A., Lindenmayer D.B., Bennett A.F., Bode M., Bradstock R.A., Cary G.J., Clarke M.F., Dexter N., Fensham R., Friend G., Gill A.M., James S., Kay G., Keith D.A., MacGregor C., Russell-Smith J., Salt D., Watson J.E.M., Williams R.J. and York A. (2010). Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation* 143: 1928-1939.

Driscoll D.A., Whitehead C.A. and Lazzari J. (2012). Spatial dynamics of the knob-tailed gecko *Nephrurus stellatus* in a fragmented agricultural landscape. *Landscape Ecology*: DOI 10.1007/s10980-10012-19734-10983

Gill A.M. and Allan G. (2008). Large fires, fire effects and the fire-regime concept. *International Journal of Wildland Fire* 17: 688-695.

Gregory N.C., Sensenig R.L. and Wilcove D.S. (2010). Effects of controlled fire and livestock grazing on bird communities in east African savannas. *Conservation Biology* 24: 1606-1616.

Keith D.A., Williams J.E. and Woinarski J.C.Z. (2002). Fire management and biodiversity conservation: key approaches and principles. In: *Flammable Australia: the fire regimes and biodiversity of a continent.* (eds. Bradstock RA, Williams JE, Gill AM). Cambridge University Press, Cambridge.

Kirkpatrick J.B., Marsden-Smedley J.B. and Leonard S.W.J. (2011). Influence of grazing and vegetation type on post-fire flammability. *Journal of Applied Ecology* 48: 642-649.

Koch A.J. and Hero J.M. (2007). The relationship between environmental conditions and activity of the giant barred frog (*Mixophyes iteratus*) on the Coomera River, south-east Queensland. *Australian Journal of Zoology* 55: 89-95.

Langlands P.R., Brennan K.E.C., Framenau V.W. and Main B.Y. (2011). Predicting the post-fire responses of animal assemblages: testing a trait-based approach using spiders. *Journal of Animal Ecology* 80: 558-568.

Lawson D.M., Regan H.M., Zedler P.H. and Franklin J. (2010). Cumulative effects of land use, altered fire regime and climate change on persistence of *Ceanothus verrucosus*, a rare, fire-dependent plant species. *Global Change Biology* 16: 2518-2529.

Letnic M., Dickman C.R., Tischler M.K., Tamayo B. and Beh C.-L. (2004). The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *Journal of Arid Environments* 59: 85-114.

Lyet A., Cheylan M., Prodon R. and Besnard A. (2009). Prescribed fire and conservation of a threatened mountain grassland specialist: a capture-recapture study on the Orsini's viper in the French alps. *Animal Conservation* 12: 238-248.

MacKenzie D.I., Nichols J.D., Sutton N., Kawanishi K. and Bailey L.L. (2005). Improving inferences in population studies of rare species that are detected imperfectly. *Ecology* 86: 1101-1113.

Manley P.N., Zielinski W.J., Schlesinger M.D. and Mori S.R. (2004). Evaluation of a multiple-species approach to monitoring species at the ecoregional scale. *Ecological Applications* 14: 296-310.

Peakall R. and Lindenmayer D.B. (2006). Genetic insights into population recovery following experimental perturbation in a fragmented landscape. *Biological Conservation* 132: 520-532.

Templeton A.R., Brazeal H. and Neuwald J.L. (2011). The transition from isolated patches to a metapopulation in the eastern collared lizard in response to prescribed fires. *Ecology* 92: 1736-1747.

Westgate M.J., Driscoll D.A. and Lindenmayer D.B. (2012). Can the intermediate disturbance hypothesis and information on species traits predict anuran responses to fire? *Oikos*: DOI 10.1111/j.1600-0706.2011.19863.x.

Whelan R.J., Rodgerson L., Dickman C.R. and Sutherland E.F. (2002). Critical life cycles of plants and animals: developing a process-based understanding of population changes in fire-prone landscapes. In: *Flammable Australia: the fire regimes and biodiversity of a continent.* (eds. Bradstock RA, Williams JE, Gill AM). Cambridge University Press, Cambridge.

Appendix A

Complete reference list

Abensperg-Traun M. and Steven D. (1997). Ant- and termite-eating in Australian mammals and lizards: a comparison. *Australian Journal of Ecology* 22: 9-17.

Alberto F. (2006). *standArich: an R package to estimate population allelic richness using standardized sample size.* CCMAR, University of the Algarve, Portugal. http://www.ccmar.ualg.pt/maree/software.php?soft=sarich.

Andersen A.N., Woinarski J.C.Z. and Parr C.L. (2012). Savanna burning for biodiversity: fire management for faunal conservation in Australian tropical savannas. *Austral Ecology*: DOI 10.1111/j.1442-9993.2011.02334.x.

Angilletta M.J., Winters R.S. and Dunham A.E. (2000). Thermal effects on the energetics of lizard embryos: implications for hatchling phenotypes. *Ecology* 81: 2957-2968.

ANVA (2001). *Australian Native Vegetation Assessment.* National Land and Water Resources Audit and Commonwealth of Australia, Canberra, ACT.

Balkenhol N., Waits L.P. and Dezzani R.J. (2009). Statistical approaches in landscape genetics: an evaluation of methods for linking landscape and genetic data. *Ecography* 32: 818-830.

Banks S.C., Blyton M.D.J., Blair D., McBurney L. and Lindenmayer D.B. (2012). Adaptive responses and disruptive effects: how major wildfire influences kinship-based social interactions in a forest marsupial. *Molecular Ecology* 21: 673-684.

Banks S.C., Dujardin M., McBurney L., Blair D., Barker M. and Lindenmayer D.B. (2011). Starting points for small mammal population recovery after wildfire: recolonisation or residual populations? *Oikos* 120: 26-37.

Banks S.C., Lindenmayer D.B., Ward S.J. and Taylor A.C. (2005). The effects of habitat fragmentation via forestry plantation establishment on spatial genotypic structure in the small marsupial carnivore, *Antechinus agilis*. *Molecular Ecology* 14: 1667-1680.

Bates A.J., Sadler J.P. and Fowles A.P. (2006). Condition-dependent dispersal of a patchily distributed riparian ground beetle in response to disturbance. *Oecologia* 150: 50-60.

Bates D., Maechler M. and Bolker B. (2011). *lme4: linear mixed-effects models using S4 classes.* R package, version 0.999375-40. http://lme4.r-forge.r-project.org/ (accessed September 2011).

Berry O., Tocher M.D., Gleeson D.M. and Sarre S.D. (2005). Effect of vegetation matrix on animal dispersal: genetic evidence from a study of endangered skinks. *Conservation Biology* 19: 855-864.

Berry O., Tocher M.D. and Sarre S.D. (2004). Can assignment tests measure dispersal? *Molecular Ecology* 13: 551-561.

Betts M.G., Hagar J.C., Rivers J.W., Alexander J.D., McGarigal K. and McComb B.C. (2010). Thresholds in forest bird occurrence as a function of the amount of early-seral broadleaf forest at landscape scales. *Ecological Applications* 20: 2116-2130.

Bonin A., Bellemain E., Bronken Eidesen P., Pompanon F., Brochmann C. and Taberlet P. (2004). How to track and assess genotyping errors in population genetics studies. *Molecular Ecology* 13: 3261-3273.

Bonnet X., Naulleau G. and Shine R. (1999). The dangers of leaving home: dispersal and mortality in snakes. *Biological Conservation* 89: 39-50.

Bowler D.E. and Benton T.G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews* 80: 205-225.

Bowman D.M.J.S., Balch J.K., Artaxo P., Bond W.J., Carlson J.M., Cochrane M.A., D'Antonio C.M., DeFries R.S., Doyle J.C., Harrison S.P., Johnston F.H., Keeley J.E., Krawchuk M.A., Kull C.A., Marston J.B., Moritz M.A., Prentice I.C., Roos C.I., Scott A.C., Swetnam T.W., van der Werf G.R. and Pyne S.J. (2009). Fire in the Earth system. *Science* 324: 481-484.

Bradstock R.A., Bedward M. and Cohn J.S. (2006). The modelled effects of differing fire management strategies on the conifer *Callitris verrucosa* within semi-arid mallee vegetation in Australia. *Journal of Applied Ecology* 43: 281-292.

Bradstock R.A., Bedward M., Gill A.M. and Cohn J.S. (2005). Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. *Wildlife Research* 32: 409-423.

Bradstock R.A. and Cohn J.S. (2002). Fire regimes and biodiversity in semi-arid mallee ecosystems. In: *Flammable Australia: the fire regimes and biodiversity of a continent.* (eds. Bradstock RA, Williams JE, Gill AM). Cambridge University Press, Cambridge.

Briani D.C., Palma A.R.T., Vieira E.M. and Henriques R.P.B. (2004). Post-fire succession of small mammals in the Cerrado of central Brazil. *Biodiversity and Conservation* 13: 1023-1037.

Brisson J.A., Strasburg J.L. and Templeton A.R. (2003). Impact of fire management on the ecology of collared lizard (*Crotaphytus collaris*) populations on the Ozark Plateau. *Animal Conservation* 6: 247-254.

Brockhurst M.A., Buckling A. and Gardner A. (2007). Cooperation peaks at intermediate disturbance. *Current Biology* 17: 761-765.

Broquet T. and Petit E.J. (2009). Molecular estimation of dispersal for ecology and population genetics. *Annual Review of Ecology, Evolution and Systematics* 40: 193-216.

Brotons L., Pons P. and Herrando S. (2005). Colonization of dynamic Mediterranean landscapes: where do birds come from after fire? *Journal of Biogeography* 32: 789-798.

Brown S., Clarke M. and Clarke R. (2009). Fire is a key element in the landscape-scale habitat requirements and global population status of a threatened bird: the mallee emu-wren (*Stipiturus mallee*). *Biological Conservation* 142: 432-445.

Burnham K.P. and Anderson D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer-Verlag, New York.

Bury R.B. (2004). Wildfire, fuel reduction, and herpetofaunas across diverse landscape mosaics in northwestern forests. *Conservation Biology* 18: 968-975.

Butz R.J. (2009). Traditional fire management: historical fire regimes and land use change in pastoral East Africa. *International Journal of Wildland Fire* 18: 442-450.

Caughley J. (1985). Effect of fire on the reptile fauna of mallee. In: *Biology of Australasian frogs and reptiles.* (eds. Grigg G, Shine R, Ehmann H), pp. 31-34. Royal Zoological Society of NSW and Surrey Beatty & Sons., Chipping Norton, NSW.

Chamaillé-Jammes S., Massot M., Aragón P. and Clobert J. (2006). Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. *Global Change Biology* 12: 392-402.

Clarke M.F. (2008). Catering for the needs of fauna in fire management: science or just wishful thinking? *Wildlife Research* 35: 385-394.

Clarke M.F., Avitabile S.C., Brown L., Callister K.E., Haslem A., Holland G.J., Kelly L.T., Kenny S.A., Nimmo D.G., Spence-Bailey L.M., Taylor R.S., Watson S.J. and Bennett A.F. (2010). Ageing mallee eucalypt vegetation after fire: insights for successional trajectories in semi-arid mallee ecosystems. *Australian Journal of Botany* 58: 363-372.

Cochrane M.A. (2001). Synergistic interactions between habitat fragmentation and fire in evergreen tropical forests. *Conservation Biology* 15: 1515-1521.

Cogger H.G. (1974). Thermal relations of the mallee dragon *Amphibolurus fordi* (Lacertilia: Agamidae). *Australian Journal of Zoology* 22: 319-339.

Cogger H.G. (1996). *Reptiles and amphibians of Australia.* Reed, Port Melbourne, VIC.

Cohn J.S. (1995). The vegetation of Nombinnie and Round Hill Nature Reserves, central-western New South Wales. *Cunninghamia* 4: 81-101.

Connell J.H. and Slatyer R.O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist* 111: 1119-1144.

Conner L.M., Castleberry S.B. and Derrick A.M. (2011). Effects of mesopredators and prescribed fire on hispid cotton rat survival and cause-specific mortality. *Journal of Wildlife Management* 75: 938-944.

Craig M.D., Grigg A.H., Garkaklis M.J., Hobbs R.J., Grant C.D., Fleming P.A. and Hardy G.E.S.J. (2009). Does habitat structure influence capture probabilities? A study of reptiles in a eucalypt forest. *Wildlife Research* 36: 509-515.

CSIRO (2011). *One-second SRTM digital elevation model.* Commonwealth Scientific and Industrial Research Organisation. http://www.csiro.au/science/One-second-SRTM-Digital-Elevation-Model.html.

Cushman S.A. and Lewis J.S. (2010). Movement behavior explains genetic differentiation in American black bears. *Landscape Ecology* 25: 1613-1625.

Cushman S.A., McKelvey K.S., Flather C.H. and McGarigal K. (2008). Do forest community types provide a sufficient basis to evaluate biological diversity? *Frontiers in Ecology and the Environment* 6: 13-17.

Cushman S.A., McKelvey K.S., Hayden J. and Schwartz M.K. (2006). Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. *The American Naturalist* 168: 486-499.

DENR (2009). *Fire Management Plan: Reserves of the Southern Eyre Peninsula.* Department of Environment and Natural Resources. http://www.environment.sa.gov.au/firemanagement/Fire_management/Fire_planning/Adopted_fire_mgt_plans (accessed September 2011).

DENR (2011). *NatureMaps* Department of Environment and Natural Resources. http://www.naturemaps.sa.gov.au/ (accessed September 2011).

DeWoody J., Nason J.D. and Hipkins V.D. (2006). Mitigating scoring errors in microsatellite data from wild populations. *Molecular Ecology Notes* 6: 951-957.

Di Stefano J., Owen L., Morris R., Duff T. and York A. (2011). Fire, landscape change and models of small mammal habitat suitability at multiple spatial scales. *Austral Ecology* 36: 638-649.

DiBattista J.D., Feldheim K.A., Garant D., Gruber S.H. and Hendry A.P. (2011). Anthropogenic disturbance and evolutionary parameters: a lemon shark population experiencing habitat loss. *Evolutionary Applications* 4: 1-17.

Didham R.K., Hammond P.M., Lawton J.H., Eggleton P. and Stork N.E. (1998). Beetle species responses to tropical forest fragmentation. *Ecological Monographs* 68: 295-323.

do Rosário I.T. and da Luz Mathias M. (2007). Post-fire recolonisation of a montado area by the endangered Cabrera vole (*Microtus cabrerae*). *International Journal of Wildland Fire* 16: 450-457.

Doak D.F., Gross K. and Morris W.F. (2005). Understanding and predicting the effects of sparse data on demographic analyses. *Ecology* 86: 1154-1163.

Doherty P.F., White G.C. and Burnham K.P. (2011). Comparison of model building and selection strategies. *Journal of Ornithology*.

Driscoll D.A. and Hardy C.M. (2005). Dispersal and phylogeography of the agamid lizard *Amphibolurus nobbi* in fragmented and continuous habitat. *Molecular Ecology* 14: 1613-1629.

Driscoll D.A. and Henderson M.K. (2008). How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model. *Biological Conservation* 141: 460-471.

Driscoll D.A., Lindenmayer D.B., Bennett A.F., Bode M., Bradstock R.A., Cary G.J., Clarke M.F., Dexter N., Fensham R., Friend G., Gill A.M., James S., Kay G., Keith D.A., MacGregor C., Possingham H.P., Russel-Smith J., Salt D., Watson J.E.M., Williams D. and York A. (2010a). Resolving conflicts in fire management using decision theory: asset-protection versus biodiversity conservation. *Conservation Letters* 3: 215-223.

Driscoll D.A., Lindenmayer D.B., Bennett A.F., Bode M., Bradstock R.A., Cary G.J., Clarke M.F., Dexter N., Fensham R., Friend G., Gill A.M., James S., Kay G., Keith D.A., MacGregor C., Russell-Smith J., Salt D., Watson J.E.M., Williams R.J. and York A. (2010b). Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation* 143: 1928-1939.

Driscoll D.A. and Roberts J.D. (1997). Impact of fuel-reduction burning on the frog *Geocrinia lutea* in southwest Western Australia. *Australian Journal of Ecology* 22: 334-339.

Driscoll D.A., Smith A.L., Blight S.R. and Maindonald J. (2012a). Reptile responses to fire and the risk of post-disturbance sampling bias. *Biodiversity and Conservation*: DOI 10.1007/s10531-10012-10267-10535.

Driscoll D.A. and Weir T. (2005). Beetle responses to habitat fragmentation depend on ecological traits, habitat condition, and remnant size. *Conservation Biology* 19: 182-194.

Driscoll D.A., Whitehead C.A. and Lazzari J. (2012b). Spatial dynamics of the knob-tailed gecko *Nephrurus stellatus* in a fragmented agricultural landscape. *Landscape Ecology*: DOI 10.1007/s10980-10012-19734-10983

Dubey S. and Shine R. (2010). Restricted dispersal and genetic diversity in populations of an endangered montane lizard (*Eulamprus leuraensis*, Scincidae). *Molecular Ecology* 19: 886-897.

Eldridge D.J. and James A.I. (2009). Soil-disturbance by native animals plays a critical role in maintaining healthy Australian landscapes. *Ecological Management and Restoration* 10: S27-S34.

Fenner A.L. and Bull C.M. (2007). Short-term impact of grassland fire on the endangered pygmy bluetongue lizard. *Journal of Zoology* 272: 444-450.

Ford W.M., Menzel M.A., McGill D.W., Laerm J. and McCay T.S. (1999). Effects of a community restoration fire on small mammals and herpetofauna in the southern Appalachians. *Forest Ecology and Management* 114: 233-243.

Fox B.J. (1982). Fire and mammalian secondary succession in an Australian coastal heath. *Ecology* 63: 1332-1341.

Frankham R. (1996). Relationship of genetic variation to population size in wildlife. *Conservation Biology* 10: 1500-1508.

Frankham R. (1997). Do island populations have less genetic variation than mainland populations? *Heredity* 78: 311-327.

Franklin D.C., Petty A.M., Williamson G.J., Brook B.W. and Bowman D.M.J.S. (2008). Monitoring contrasting land management in the savanna landscapes of northern Australia. *Environmental Management* 2008.

Friend G.R. (1993). Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: a review. *Biological Conservation* 65: 99-114.

Fuller S.J., Bull C.M., Murray K. and Spencer R.J. (2005). Clustering of related individuals in a population of the Australian lizard, *Egernia frerei*. *Molecular Ecology* 14: 1207-1213.

Funk W.C., Donnelly M.A. and Lips K.R. (2005). Alternative views of amphibian toe-clipping. *Nature* 433: 193.

Gamble T. (2010). A review of sex determining mechanisms in geckos (Gekkota: Squamata). *Sexual Development* 4: 88-103.

Gardner M.G., Bull C.M., Cooper S.J.B. and Duffield G.A. (2001). Genetic evidence for a family structure in stable social aggregations of the Australian lizard *Egernia stokesii*. *Molecular Ecology* 10: 175-183.

Gardner M.G., Cooper S.J.B., Bull C.M. and Grant W.N. (1999). Isolation of microsatellite loci from a social lizard, *Egernia stokesii*, using a modified enrichment procedure. *The Journal of Heredity* 90: 301-304.

Gardner M.G., Sanshez J.J., Dudaniec R.Y., Rheinberger L., Smith A.L. and Saint K.M. (2008). *Tiliqua rugosa* microsatellites: isolation via enrichment and characterisation of loci for multiplex PCR in *T. rugosa* and the endangered *T. adelaidensis*. *Conservation Genetics* 9: 233-237.

Gill A.M. (1975). Fire and the Australian flora: a review. *Australian Forestry* 38: 4-25.

Gill A.M. and Allan G. (2008). Large fires, fire effects and the fire-regime concept. *International Journal of Wildland Fire* 17: 688-695.

Godfrey S.S. and Hutchinson M.N. (2010). Notes on diet and reproductive condition of *Ctenotus* (Scincidae) of the mallee of South Australia. *Herpetofauna* 40: 2-8.

Goodyear S.E. and Pianka E.R. (2008). Sympatric ecology of five species of fossorial snakes (Elapidae) in Western Australia. *Journal of Herpetology* 42: 279-285.

Goslee S.C. and Urban D.L. (2007). The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software* 22: 1-19.

Greenberg C.H., Neary D.G. and Harris L.D. (1994). Effect of high-intensity wildfire and silvicultural treatments on reptile communities in sand-pine scrub. *Conservation Biology* 8: 1047-1057.

Gregory N.C., Sensenig R.L. and Wilcove D.S. (2010). Effects of controlled fire and livestock grazing on bird communities in east African savannas. *Conservation Biology* 24: 1606-1616.

Griffiths A.D. (1999). Demography and home range of the frillneck lizard, *Chlamydosaurus kingii* (Agamidae), in northern Australia. *Copeia* 1999: 1089-1096.

Griffiths A.D. and Christian K.A. (1996). The effects of fire on the frillneck lizard (*Chlamydosaurus kingii*) in northern Australia. *Australian Journal of Ecology* 21: 386-398.

Guillot G., Estoup A., Mortier F. and Cosson J.-F. (2005). A spatial statistical model for landscape genetics. *Genetics* 170: 1261-1280.

Hanski I. (1998). Metapopulation dynamics. *Nature* 396: 41-49.

Hardy O.J. and Vekemans X. (2002). SPAGEDI: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Molecular Ecology Notes* 2: 618-620.

Haslem A., Kelly L.T., Nimmo D.G., Watson S.J., Kenny S.A., Taylor R.S., Avitabile S.C., Callister K.E., Spence-Bailey L.M., Clarke M.F. and Bennett A.F. (2011). Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. *Journal of Applied Ecology* 48: 247-256.

Hawlena D., Saltz D., Abramsky Z. and Bouskila A. (2010). Ecological trap for desert lizards caused by anthropogenic changes in habitat structure that favor predator activity. *Conservation Biology* 24: 803-809.

Hayden M.J., Nguyen T.M., Waterman A. and Chalmers K.J. (2008). Multiplex-Ready PCR: A new method for multiplexed SSR and SNP genotyping. *BMC Genomics* 9: 80.

Hines J.E. (1996). *RDSURVIV User's Manual.* Biological Resources Division, USGS. http://www.mbr-pwrc.usgs.gov/software/rdsurviv.html (accessed September 2011).

Hochberg Y. (1988). A sharper Bonferroni procedure for multiple tests of significance. *Biometrika* 75: 800-802.

Hoehn M., Sarre S. and Henle K. (2007). The tales of two geckos: does dispersal prevent extinction in recently fragmented populations? *Molecular Ecology* 16: 3299-3312.

Holland G.J. and Bennett A.F. (2011). Recolonization of forest fragments by a native rodent following experimental 'extinctions'. *Austral Ecology* 36: 521-529.

Hossack B.R., Eby L.A., Guscio C.G. and Corn P.S. (2009). Thermal characteristics of amphibian microhabitats in a fire-disturbed landscape. *Forest Ecology and Management* 258: 1414-1421.

Hutchinson M.F. (2011). *ANUDEM Version 5.3* Fenner School of Environment and Society, ANU. http://fennerschool.anu.edu.au/research/publications/software-datasets/anudem.

Keith D.A. and Henderson M.K. (2002). Restoring the prepastoral condition: response to Jurskis. *Austral Ecology* 27: 691-693.

Keith D.A., Holman L., Rodoreda S., Lemmon J. and Bedward M. (2007). Plant functional types can predict decade-scale changes in fire-prone vegetation. *Journal of Ecology* 95: 1324-1337.

Keith D.A., Williams J.E. and Woinarski J.C.Z. (2002). Fire management and biodiversity conservation: key approaches and principles. In: *Flammable Australia: the fire regimes and biodiversity of a continent.* (eds. Bradstock RA, Williams JE, Gill AM). Cambridge University Press, Cambridge.

Keller L.F. and Waller D.M. (2002). Inbreeding effects in wild populations. *Trends in Ecology and Evolution* 17: 230-241.

Kelly L.T., Nimmo D.G., Spence-Bailey L.M., Haslem A., Watson S.J., Clarke M.F. and Bennett A.F. (2011). Influence of fire history on small mammal distributions: insights from a 100-year post-fire chronosequence. *Diversity and Distributions* 17: 462-473.

Kendall W.L. and Hines J.E. (1999). Program RDSURVIV: an estimation tool for capture-recapture data collected under Pollock's robust design. *Bird Study* 46: S32-S38.

Kendall W.L., Nichols J.D. and Hines J.E. (1997). Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78: 563-578.

Kendall W.L., Pollock K.H. and Brownie C. (1995). A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. *Biometrics* 51: 293-308.

Kirkpatrick J.B., Marsden-Smedley J.B. and Leonard S.W.J. (2011). Influence of grazing and vegetation type on post-fire flammability. *Journal of Applied Ecology* 48: 642-649.

Kisdi É. (2002). Dispersal: risk spreading versus local adaptation. *The American Naturalist* 159: 579-596.

Knight T.M. and Holt R.D. (2005). Fire generates spatial gradients in herbivory: an example from a Florida sandhill ecosystem. *Ecology* 86: 587-593.

Koch A.J. and Hero J.M. (2007). The relationship between environmental conditions and activity of the giant barred frog (*Mixophyes iteratus*) on the Coomera River, south-east Queensland. *Australian Journal of Zoology* 55: 89-95.

Konvicka M., Zimmermann K., Klimova M., Hula V. and Fric Z. (2012). Inverse link between density and dispersal distance in butterflies: field evidence from six co-occurring species. *Population Ecology* 54: 91-101.

Kuchling G. (2007). Impact of fuel reduction burns and wildfires on the critically endangered western swamp tortoise *Peudemydura umbrina. Ecological Society of Australia Conference Proceedings,* Perth, Western Australia.

Laake J. and Rexstad E. (2008). RMark – an alternative approach to building linear models in MARK. In: *Program MARK: A Gentle Introduction, 7th Ed.* (eds. Cooch EG, White GC), pp. C1-C115. Available from: http://www.phidot.org/software/mark/docs/book/.

Landguth E.L., Cushman S.A., Schwartz M.K., McKelvey K.S., Murphy M. and Luikart G. (2010). Quantifying the lag time to detect barriers in landscape genetics. *Molecular Ecology* 19: 4179-4191.

Lange R., Diekötter T., Schiffmann L.A., Wolters V. and Durka W. (2012). Matrix quality and habitat configuration interactively determine functional connectivity in a widespread bush cricket at a small spatial scale. *Landscape Ecology* 27: 381-392.

Langkilde T. and Shine R. (2006). How much stress do researchers inflict on their study animals? A case study using a scincid lizard, *Eulamprus heatwolei. The Journal of Experimental Biology* 209: 1035-1043.

Langlands P.R., Brennan K.E.C., Framenau V.W. and Main B.Y. (2011). Predicting the post-fire responses of animal assemblages: testing a trait-based approach using spiders. *Journal of Animal Ecology* 80: 558-568.

Lawson D.M., Regan H.M., Zedler P.H. and Franklin J. (2010). Cumulative effects of land use, altered fire regime and climate change on persistence of *Ceanothus verrucosus*, a rare, fire-dependent plant species. *Global Change Biology* 16: 2518-2529.

Le Galliard J.-F., Ferrière R. and Clobert J. (2005). Juvenile growth and survival under dietary restriction: are males and females equal? *Oikos* 111: 368-376.

Leberg P.L. (2002). Estimating allelic richness: effects of sample size and bottlenecks. *Molecular Ecology* 11: 2445-2449.

Lebreton J.-D., Burnham K.P., Clobert J. and Anderson D.R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62: 67-118.

Lee-Yaw J.A., Davidson A., McRae B.H. and Green D.M. (2009). Do landscape processes predict phylogeographic patterns in the wood frog? *Molecular Ecology* 18: 1863-1874.

Legendre P., Lapointe F.-J. and Casgrain P. (1994). Modeling brain evolution from behavior: a permutational regression approach. *Evolution* 48: 1487-1499.

Leidner A.K. and Haddad N.M. (2011). Combining measures of dispersal to identify conservation strategies in fragmented landscapes. *Conservation Biology* 25: 1022-1031.

Letnic M., Dickman C.R., Tischler M.K., Tamayo B. and Beh C.-L. (2004). The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *Journal of Arid Environments* 59: 85-114.

Levy E., Kennington W.J., Tomkins J.L. and LeBas N.R. (2010). Land clearing reduces gene flow in the granite outcrop-dwelling lizard, *Ctenophorus ornatus*. *Molecular Ecology* 19: 4192-4203.

Lindenmayer D.B., Likens G.E. and Franklin J.F. (2010). Rapid responses to facilitate ecological discoveries from major disturbances. *Frontiers in Ecology and the Environment* 8: 527-532.

Lindenmayer D.B., Wood J.T., MacGregor C., Michael D.R., Cunningham R.B., Crane M., Montague-Drake R., Brown D., Muntz R. and Driscoll D.A. (2008). How predictable are reptile responses to wildfire? *Oikos* 117: 1086-1097.

Lyet A., Cheylan M., Prodon R. and Besnard A. (2009). Prescribed fire and conservation of a threatened mountain grassland specialist: a capture-recapture study on the Orsini's viper in the French alps. *Animal Conservation* 12: 238-248.

MacKenzie D.I., Nichols J.D., Sutton N., Kawanishi K. and Bailey L.L. (2005). Improving inferences in population studies of rare species that are detected imperfectly. *Ecology* 86: 1101-1113.

Maindonald J.H. and Braun W.J. (2010). *Data analysis and graphics using R: an example-based approach*, 3rd edn., Cambridge University Press.

Manley P.N., Zielinski W.J., Schlesinger M.D. and Mori S.R. (2004). Evaluation of a multiple-species approach to monitoring species at the ecoregional scale. *Ecological Applications* 14: 296-310.

Martins E.P. (1994). Phylogenetic perspectives on the evolution of lizard territoriality. In: *Lizard Ecology: Historical and Experimental Perspectives.* (eds. Vitt LJ, Pianka ER), pp. 117-144. Princeton University Press, Princeton, N.J.

Masters P. (1996). The effects of fire-driven succession on reptiles in spinifex grasslands at Uluru National Park, Northern Territory. *Wildlife Research* 23: 39-48.

Mazerolle M.J. (2011). *AICcmodavg.* R package, version 1.2. http://cran.r-project.org/web/packages/AICcmodavg/index.html (accessed September 2011).

McRae B.H. and Beier P. (2007). Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Science USA* 104: 19885-19890.

Meglécz E. (2007). MICROFAMILY (version 1): a computer program for detecting flanking-region similarities among different microsatellite loci. *Molecular Ecology Notes* 7: 18-20.

Meglécz E., Costedoat C., Debut V., Gilles A., Malausa T., Pech N. and Martin J.-F. (2010). QDD: a user-friendly program to select microsatellite markers and design primers from large sequencing projects. *Bioinformatics* 26: 403-404.

Mills L.S. and Allendorf F.W. (1996). The one-migrant-per-generation rule in conservation and management. *Conservation Biology* 10: 1509-1518.

Moreira F., Catry F., Duarte I., Acácio V. and Silva J.S. (2009). A conceptual model of sprouting responses in relation to fire damage: an example with cork oak (*Quercus suber* L.) trees in southern Portugal. *Plant Ecology* 201: 77-85.

Moreira F., Viedma O., Arianoutsou M., Curt T., Koutsias N., Rigolot E., Barbati A., Corona P., Vaz P., Xanthopoulos G., Mouillot F. and Bilgili E. (2011). Landscape-wildfire interactions in southern Europe: implications for landscape management. *Journal of Environmental Management* 92: 2389-2402.

Moretti M., de Bello F., Roberts S.P.M. and Potts S.G. (2009). Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. *Journal of Animal Ecology* 78: 98-108.

Murphy A.R., Gardner M.G. and Fox S.F. (2009). Isolation of microsatellites via enrichment and a sequence tagged method in a South American lizard with suspected parental care, *Liolaemus leopardinus*. *Conservation Genetics Resources* 1: 13-16.

Murphy M.A., Evans J.S. and Storfer A. (2010a). Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. *Ecology* 91: 252-261.

Murphy S.A., Legge S.M., Heathcote J. and Mulder E. (2010b). The effects of early and late-season fires on mortality, dispersal, physiology and breeding of red-backed fairy-wrens (*Malurus melanocephalus*). *Wildlife Research* 37: 145-155.

Mushinsky H.R. (1985). Fire and the Florida sandhill herpetofaunal community: with special attention to responses of *Cnemidophorus sexlineatus*. *Herpetologica* 41: 333-342.

O'Brien T.G., Kinnaird M.F., Nurcahyo A., Prasetyaningrum M. and Iqbal M. (2003). Fire, demography and the persistence of siamang (*Symphalangus syndactylus*: Hylobatidae) in a Sumatran rainforest. *Animal Conservation* 6: 115-121.

Olsson M., Wapstra E., Swan G., Snaith E., Clarke R. and Madsen T. (2005). Effects of long-term fox baiting on species composition and abundance in an Australian lizard community. *Austral Ecology* 30: 899-905.

Otis D.L., Burnham K.P., White G.C. and Anderson D.R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62: 1-135.

Pardon L.G., Brook B.W., Griffiths A.D. and Braithwaite R.W. (2003). Determinants of survival for the northern brown bandicoot under a landscape-scale fire experiment. *Journal of Animal Ecology* 72: 106-115.

Parr C.L. and Andersen A.N. (2006). Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Conservation Biology* 20: 1610-1619.

Parsons B.C. and Gosper C.R. (2011). Contemporary fire regimes in a fragmented and an unfragmented landscape: implications for vegetation structure and persistence of the fire-sensitive malleefowl. *International Journal of Wildland Fire* 20: 184-194.

Pausas J.G., Bradstock R.A., Keith D.A., Keeley J.E. and GCTE (2004). Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* 85: 1085-1100.

Pausas J.G. and Lloret F. (2007). Spatial and temporal patterns of plant functional types under simulated fire regimes. *International Journal of Wildland Fire* 16: 484-492.

Peakall R. and Lindenmayer D.B. (2006). Genetic insights into population recovery following experimental perturbation in a fragmented landscape. *Biological Conservation* 132: 520-532.

Peakall R. and Smouse P.E. (2006). GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* 6: 288-295.

Perry R.W., Rudolph D.C. and Thill R.E. (2009). Reptile and amphibian responses to restoration of fire-maintained pine woodlands. *Restoration Ecology* 17: 917-927.

Peters R.A. and Ord T.J. (2003). Display response of the Jacky Dragon, *Amphibolurus muricatus* (Lacertilia: Agamidae), to intruders: a semi-Markovian process. *Austral Ecology* 28: 499-506.

Petty A., Alderson J., Muller R., Scheibe O., Wilson K. and Winderlich S. (2007). *Arnhemland Plateau Draft Fire Management Plan.* Kakadu National Park. http://www.environment.gov.au/parks/publications/kakadu/fire-management-plan.html (accessed September 2011).

Pianka E.R. (1969a). Habitat specificity, speciation, and species density in Australian desert lizards. *Ecology* 50: 498-502.

Pianka E.R. (1969b). Sympatry of desert lizards (*Ctenotus*) in Western Australia. *Ecology* 50: 1012-1030.

Pianka E.R. (1970). On *r*- and *K*-selection. *The American Naturalist* 104: 592-597.

Pianka E.R. (1972). Zoogeography and speciation of Australian desert lizards: an ecological perspective. *Copeia* 1972: 127-145.

Pianka E.R. and Pianka H.D. (1976). Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australian desert. *Copeia* 1976: 125-142.

Piggott M.P., Banks S.C. and Taylor A.C. (2006). Population structure of brush-tailed rock-wallaby (*Petrogale penicillata*) colonies inferred from analysis of faecal DNA. *Molecular Ecology* 15: 93-105.

Pike D.A., Webb J.K. and Shine R. (2010). Nesting in a thermally challenging environment: nest-site selection in a rock-dwelling gecko, *Oedura lesueurii* (Reptilia: Gekkonidae). *Biological Journal of the Linnean Society* 99: 250-259.

Pike D.A., Webb J.K. and Shine R. (2011). Removing forest canopy cover restores a reptile assemblage. *Ecological Applications* 21: 274-280.

Pollock K.H. (1982). A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46: 752-757.

Pollock K.H., Nichols J.D., Brownie C. and Hines J.E. (1990). Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107: 1-97.

Pons P. and Clavero M. (2010). Bird responses to fire severity and time since fire in managed mountain rangelands. *Animal Conservation* 13: 294-305.

Porter A.H. (1999). Refugees from lost habitat and reorganization of genetic population structure. *Conservation Biology* 13: 850-859.

Pradel R. (1996). Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52: 703-709.

Prevedello J.A., Forero-Medina G. and Vieira M.V. (2010). Movement behaviour within and beyond perceptual ranges in three small mammals: effects of matrix type and body mass. *Journal of Animal Ecology* 79: 1315-1323.

Pritchard J.K., Stephens M. and Donnelly P. (2000). Inference of population structure using multilocus genotype data. *Genetics* 155: 945-959.

Pritchard J.K., Wen X. and Falush D. (2007). *Documentation for structure software: version 2.2.* http://pritch.bsd.uchicago.edu/structure.html.

Quinn G.P. and Keough M.J. (2002). *Experimental Design and Data Analysis for Biologists.* Cambridge University Press, Cambridge.

R Development Core Team (2011). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Raymond M. and Rousset F. (1995). GENEPOP (Version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity* 86: 248-249.

Robinet C., Lance D.R., Thorpe K.W., Onufrieva K.S., Tobin P.C. and Liebhold A.M. (2008). Dispersion in time and space affect mating success and Allee effects in invading gypsy moth populations. *Journal of Animal Ecology* 77: 966-973.

Robinson A.C. and Heard M.B. (1985). National Parks. In: *Natural history of Eyre Peninsula.* (eds. Twidale CR, Tyler MJ, Davies M). Royal Society of South Australia, Adelaide, SA.

Rochester C.J., Berehme C.S., Clark D.R., Stokes D.C., Hathaway S.A. and Fisher R.N. (2010). Reptile and amphibian responses to large-scale wildfires in southern California. *Journal of Herpetology* 44: 333-351.

Rousset F. (2000). Genetic differentiation between individuals. *Journal of Evolutionary Biology* 13: 58-62.

Saccheri I., Kuussaari M., Kankare M., Vikman P., Fortelius W. and Hanski I. (1998). Inbreeding and extinction in a butterfly metapopulation. *Nature* 392: 491-494.

Sanz-Aguilar A., Anadón J.D., Giménez A., Ballestar R., Graciá E. and Oro D. (2011). Coexisting with fire: the case of the terrestrial tortoise *Testudo graeca* in mediterranean shrublands. *Biological Conservation* 144: 1040-1049.

Sarà M., Bellia E. and Milazzo A. (2006). Fire disturbance disrupts co-occurrence patterns of terrestrial vertebrates in Mediterranean woodlands. *Journal of Biogeography* 33: 843-852.

Schlesinger C.A. (2007). Does vegetation cover affect the rate of capture of ground-active lizards in pitfall traps? *Wildlife Research* 34: 359-365.

Schlesinger C.A., Noble J.C. and Weir T. (1997). Fire studies in mallee (*Eucalyptus spp.*) communities of western New South Wales: reptile and beetle populations in sites of differing fire history. *Rangeland Journal* 19: 190-205.

Schmuki C., Vorburger C., Runciman D., Maceachern S. and Sunnucks P. (2006). When log-dwellers meet loggers: impacts of forest fragmentation on two endemic log-dwelling beetles in southeastern Australia. *Molecular Ecology* 15: 1481-1492.

Schooley R. and Wiens J.A. (2004). Movements of cactus bugs: patch transfers, matrix resistance, and edge permeability. *Landscape Ecology* 19: 801-810.

Schrey A.W., Fox A.M., Mushinsky H.R. and McCoy E.D. (2011). Fire increases variance in genetic characteristics of Florida Sand Skink (*Plestiodon reynoldsi*) local populations. *Molecular Ecology* 20: 56-66.

Schtickzelle N., Joiris A., Van Dyck H. and Baguette M. (2007). Quantitative analysis of changes in movement behaviour within and outside habitat in a specialist butterfly. *BMC Evolutionary Biology* 7: 4.

Schtickzelle N., Mennechez G. and Baguette M. (2006). Dispersal depression with habitat fragmentation in the bog fritillary butterfly. *Ecology* 87: 1057-1065.

Schwerdtfeger P. (1985). Climate. In: *Natural history of Eyre Peninsula.* (eds. Twidale CR, Tyler MJ, Davies M), pp. 89-104. Royal Society of South Australia, Adelaide, SA.

Shanahan D.F., Possingham H.P. and Riginos C. (2011). Models based on individual level movement predict spatial patterns of genetic relatedness for two Australian forest birds. *Landscape Ecology* 26: 137-148.

Shine R. (1980). "Costs" of reproduction in reptiles. *Oecologia* 46: 92-100.

Short Bull R.A., Cushman S.A., Mace R., Chilton T., Kendall K.C., Landguth E.L., Schwartz M.K., McKelvey K., Allendorf F.W. and Luikart G. (2011). Why replication is important in landscape genetics: American black bear in the Rocky Mountains. *Molecular Ecology* 20: 1092-1107.

Smith A.L., Bull C.M. and Driscoll D.A. (2012). Post-fire succession affects abundance and survival but not detectability in a knob-tailed gecko. *Biological Conservation* 145: 139-147.

Smith A.L., Bull C.M. and Driscoll D.A. (Chapter 3). A six-year study reveals previously undetected responses to fire in reptiles. In: *Reptile dispersal and demographics after fire: process-based knowledge to assist fire management for biodiversity*. Submitted PhD thesis, The Australian National University.

Smith A.L., Bull C.M., Gardner M.G. and Driscoll D.A. (Chapter 7). Spatial and temporal variation in genetic structure of lizards in landscapes with complex fire mosaics. . In: *Reptile dispersal and demographics after fire: process-based knowledge to assist fire management for biodiversity*. Submitted PhD thesis, The Australian National University.

Smith A.L., Gardner M.G., Bull C.M. and Driscoll D.A. (2011). Primers for novel microsatellite markers in "fire-specialist" lizards (*Amphibolurus norrisi, Ctenotus atlas* and *Nephrurus stellatus*) and their performance across multiple populations. *Conservation Genetics Resources* 3: 345-350.

Smith A.L., Gardner M.G., Bull C.M. and Fenner A.L. (2009). Restricted gene flow in the endangered pygmy bluetongue lizard (*Tiliqua adelaidensis*) in a fragmented agricultural landscape. *Wildlife Research* 36: 466-478.

Smith L.M. and Burgoyne L.A. (2004). Collecting, archiving and processing DNA from wildlife samples using FTA(R) databasing paper. *BMC Ecology* 4: http://www.biomedcentral.com/1472-6785/1474/1474.

South S.L. (2010). *Natural history and spatial ecology of Amphibolurus norrisi in southern Australia.* Unpublished honours thesis, Flinders University, Adelaide.

Spear S.F. and Storfer A. (2010). Anthropogenic and natural disturbance lead to differing patterns of gene flow in the Rocky Mountain tailed frog, *Ascaphus montanus*. *Biological Conservation* 143: 778-786.

Specht R.L. (1972). *The Vegetation of South Australia.* AB James, Government Printer, Adelaide, SA.

Stanley T.R. and Richards J.D. (2005). Software review: a program for testing capture-recapture data for closure. *Wildlife Society Bulletin* 33: 782-785.

Stephens P.A., Sutherland W.J. and Freckleton R.P. (1999). What is the Allee effect? *Oikos* 87: 185-190.

Storfer A., Murphy M.A., Spear S.F., Holderegger R. and Waits L.P. (2010). Landscape genetics: where are we now? *Molecular Ecology* 19: 3496-3514.

Stow A., Silberbauer L., Beattie A.J. and Briscoe D.A. (2007). Fine-scale genetic structure and fire-created habitat patchiness in the Australian allodapine bee, *Exoneura nigrescens* (Hymenoptera: Apidae). *Journal of Heredity* 98: 60-66.

Stow A.J. and Sunnucks P. (2004). High mate and site fidelity in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. *Molecular Ecology* 13: 419-430.

Stow A.J., Sunnucks P., Briscoe D.A. and Gardner M.G. (2001). The impact of habitat fragmentation on dispersal in Cunningham's skink (*Egernia cunninghami*): evidence from allelic and genotypic analyses of microsatellites. *Molecular Ecology* 10: 867-878.

Sumner J., Jessop T., Paetkau D. and Moritz C. (2004). Limited effect of anthropogenic habitat fragmentation on molecular diversity in a rain forest skink, *Gnypetoscincus queenslandiae*. *Molecular Ecology* 13: 259-269.

Sumner J., Rousset F., Estoup A. and Moritz C. (2001). 'Neighbourhood' size, dispersal and density estimates in the prickly forest skink (*Gnypetoscincus queenslandiae*) using individual genetic and demographic methods. *Molecular Ecology* 10: 1917-1927.

Sutton J.T., Nakagawa S., Robertson B.C. and Jamieson I.G. (2011). Disentangling the roles of natural selection and genetic drift in shaping variation at MHC immunity genes. *Molecular Ecology* 20: 4408-4420.

Tabarelli M. and Gascon C. (2005). Lessons from fragmentation research: improving management and policy guidelines for biodiversity conservation. *Conservation Biology* 19: 734-739.

Teasdale L.C., Smith A.L., Thomas M., Whitehead C.A. and Driscoll D.A. (in review). Detecting invertebrate responses to fire depends on sampling method and taxonomic resolution in an Australian mallee woodland. *Austral Ecology*.

Templeton A.R., Brazeal H. and Neuwald J.L. (2011). The transition from isolated patches to a metapopulation in the eastern collared lizard in response to prescribed fires. *Ecology* 92: 1736-1747.

Templeton A.R., Robertson R.J., Brisson J. and Strasburg J. (2001). Disrupting evolutionary processes: the effect of habitat fragmentation on collared lizards in the Missouri Ozarks. *Proceedings of the National Academy of Science, USA.* 98: 5426-5432.

Thomas C.D. (2000). Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 267: 139-145.

Travis J.M.J. (2003). Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270: 467-473.

Travis J.M.J. and Dytham C. (1999). Habitat persistence, habitat availability and the evolution of dispersal. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 266: 723-728.

Turner M.G., Wu Y., Wallace L.L., Romme W.H. and Brenkert A. (1994). Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. *Ecological Applications* 4: 472-496.

Twidale C.R. and Campbell E.M. (1985). The form of the land surface. In: *Natural history of Eyre Peninsula.* (eds. Twidale CR, Tyler MJ, Davies M). Royal Society of South Australia, Adelaide, SA.

van Nouhuys S. and Hanski I. (2002). Colonization rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape. *Journal of Animal Ecology* 71: 639-650.

Van Oosterhout C., Hutchinson W.F., Wills D.P.M. and Shipley P. (2004). MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes* 4: 535-538.

VBRC (2010). Fire preparation, response and recovery. Final Report, Volume II. http://www.royalcommission.vic.gov.au/Commission-Reports/Final-Report.

Vernes K. and Haydon D.T. (2001). Effect of fire on northern bettong (*Bettongia tropica*) foraging behaviour. *Austral Ecology* 26: 649-659.

Vilà-Cabrera A., Saura-Mas S. and Lloret F. (2008). Effects of fire frequency on species composition in a Mediterranean shrubland. *Écoscience* 15: 519-528.

Waichman A.V. (1992). An alphanumeric code for toe clipping amphibians and reptiles. *Herpetological Review* 23: 19-21.

Walker F.M., Sunnucks P. and Taylor A.C. (2008). Evidence for habitat fragmentation altering within-population processes in wombats. *Molecular Ecology* 17: 1674-1684.

Wang X. and Cumming S.G. (2010). Configuration dynamics of boreal forest landscapes under recent fire and harvesting regimes in western Canada. *Landscape Ecology* 25: 1419-1432.

Warner D.A. and Shine R. (2009). Maternal and environmental effects on offspring phenotypes in an oviparous lizard: do field data corroborate laboratory data? *Oecologia* 161: 209-220.

Welsh A.H. (1996). *Aspects of Statistical Inference* John Wiley & Sons, Inc., New York.

Westgate M.J., Driscoll D.A. and Lindenmayer D.B. (2012). Can the intermediate disturbance hypothesis and information on species traits predict anuran responses to fire? *Oikos*: DOI 10.1111/j.1600-0706.2011.19863.x.

Whelan R.J., Rodgerson L., Dickman C.R. and Sutherland E.F. (2002). Critical life cycles of plants and animals: developing a process-based understanding of population changes in fire-prone landscapes. In: *Flammable Australia: the fire regimes and biodiversity of a continent.* (eds. Bradstock RA, Williams JE, Gill AM). Cambridge University Press, Cambridge.

White G.C. (2005). Correcting wildlife counts using detection probabilities. *Wildlife Research* 32: 211-216.

White G.C. and Burnham K.P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* 46: 120-138.

White P.S. and Pickett S.T.A. (1985). Natural disturbance and patch dynamics: an introduction. In: *The Ecology of Natural Disturbance and Patch Dynamics.* (eds. Pickett STA, White PS), pp. 3-13. Academic Press, San Diego, USA.

Williams J.R., Driscoll D.A. and Bull C.M. (2011). Roadside connectivity does not increase reptile abundance or richness in a fragmented mallee landscape. *Austral Ecology*.

Wilson S. and Swan G. (2008). *A Complete Guide to Reptiles of Australia*, 2 edn. New Holland, Sydney.

Wilson S. and Swan G. (2010). *A Complete Guide to Reptiles of Australia*, 3 edn. New Holland, Sydney.

Wilson T.L., Johnson E.J. and Bissonette J.A. (2009). Relative importance of habitat area and isolation for bird occurrence patterns in a naturally patchy landscape. *Landscape Ecology* 24: 351-360.

Woinarski J.C.Z., Armstrong M., Price O., McCartney J., Griffiths A.D. and Fisher A. (2004a). The terrestrial vertebrate fauna of Litchfield National Park, Northern Territory: monitoring over a 6-year period and response to fire history. *Wildlife Research* 31: 587-596.

Woinarski J.C.Z., Legge S., Fitzsimons J.A., Traill B.J., Burbidge A.A., Fisher A., Firth R.S.C., Gordon I.J., Griffiths A.D., Johnson C.N., McKenzie N.L., Palmer C., Radford I., Rankmore B., Ritchie E.G., Ward S. and Ziembicki M. (2011). The disappearing mammal fauna of northern Australia: context, cause, and response. *Conservation Letters* 4: 192-201.

Woinarski J.C.Z., Risler J. and Kean L. (2004b). Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical *Eucalyptus* open forest, Northern Territory, Australia. *Austral Ecology* 29: 156-176.

Woolley L., Millspaugh J.J., Woods R.J., Janse van Rensburg S., Mackey R.L., Page B. and Slotow R. (2008). Population and individual elephant response to a catastrophic fire in Pilanesberg National Park. *PLoS ONE* 3: e3233.

Wright S. (1943). Isolation by distance. *Genetics* 28: 114-138.

Zuur A.F., Ieno E.N., Walker N.J., Saveliev A.A. and Smith G.M. (2009). *Mixed effects models and extensions in ecology with R.* Springer, New York.